ON THE EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF ORNAMENTAL TRAITS: THE FUNCTION AND VARIABILITY OF THE VISUAL AND ACOUSTIC DISPLAYS OF AUKLETS (AETHIINI, ALCIDAE, CHARADRIIFORMES)

SAMPATH SUMEDHA SENEVIRATNE


CENTRE FOR NFLD. STUDIES
MEMORIAL UNIVERSITY
OF NEWFOUNDLAND

ON THE EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF ORNAMENTAL TRAITS: THE FUNCTION AND VARIABILITY OF THE VISUAL AND ACOUSTIC DISPLAYS OF AUKLETS (AETHIINI, ALCIDAE, CHARADRIIFORMES)

BY

© SAMPATH SUMEDHA SENEVIRATNE

A THESIS

SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR

THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGY

MEMORIAL UNIVERSITY OF NEWFOUNDLAND

2008

ST. JOHN'S, NEWFOUNDLAND AND LABRADOR, CANADA

ABSTRACT

The occurrence of extravagant display traits in animals can be explained by their phylogenetic history, and adaptations to the physical and social environment. None of these processes are mutually exclusive, however. The primary objective of my study was to elucidate the roles of such processes on evolution of ornamental and vocal traits in a monophyletic group of North Pacific seabirds - the auklets (Alcidae, Aethiini). Sexual selection has been the main explanation for the evolution of feather ornaments such as the elongated facial plumes of auklets. My experimental evidence pointed towards a mechanosensory use for the long facial plumes of Whiskered Auklet (*Aethia pygmaea*), a crevice dwelling and nocturnal seabird. While navigating inside a lightproof maze simulating the conditions of breeding crevices, Whiskered Auklets had more than double the frequency of head bumps (275%) in the absence of the protruding feathers. Tracing the phylogenetic pattern in several closely related auklet species (*Aethia*) revealed that only the ornamented younger species that breed in deep crevices have the mechanosensory ability. A pairwise analysis across all non-passerine bird families suggested a greater frequency of long facial plumes in species that live in complex habitats or active in low light conditions. Birds inhabiting cluttered environments would benefit from projecting long facial plumage that mechanically detects obstacles. Thus, once the primordial mechanosensory feather structures evolved through the selective pressure enforced by the habitat, sexual and other selection processes may have acted on these traits and led towards further elaboration. Vocal repertoires of breeding auklets were categorized and quantified to provide a baseline for a comparative study of the evolution of vocalization. Similar to their visual display, auklet vocal repertoires were complex and large (~25 display types across species) with 3-5 vocal display types for each species. There were vocal homologies in the frequency modulation of notes, and arrangement and composition of note types in display. Unlearned vocalizations of non-oscine birds such as auklets' are likely to be informative as to phylogenetic affinities. To test the hypothesis that phylogenetic relationships are the major determinant of vocal

evolution in auklets, large number of vocal and syringeal characters were mapped onto a molecular phylogeny based on a combination of mitochondrial and nuclear DNA characters. Low Consistency and Retention Indices (CI = 0.70, RI = 0.10) indicated a poor fit between molecular and vocal phylogeny. Temporal and syringeal attributes showed a greater congruence with molecular trees than do frequency attributes. A combination of factors including phylogenetic relatedness, visual ornaments, and the acoustic properties of the breeding habitat may have played roles in vocal divergence in auklets. Taken together, these results indicated a complex evolutionary pattern in visual and vocal display in Aethiini, suggesting that although visual and vocal display have evolved in close association with species divergence, natural and sexual selection have created patterns across species that are at odds with phylogeny.

DEDICATION

"You need time for this kind of activity,

Nature cannot be studied in depth, if you are in a hurry..."

Bruce Henry – Birder/wildlife painter

(Son of G. M. Henry - a Sri Lankan entomologist/ornithologist/wildlife painter)

It may take even longer than a generation to fully appreciate the true beauty of the living world.

This dissertation is a milestone of one such long journey **MY DEAR PARENTS** have started.

They, not only provided me the genes for my deep fascination of animals, but also made our home - **SERENGETI** - a cradle for naturalists.

ACKNOWLEDGEMENTS

So much happened in a so little time since the day I left Sri Lanka to pursue my postgraduate studies. This dissertation represents the pinnacle of this adventurous, stressful yet thoroughly enjoyable learning endeavor that far exceeded all my childhood dreams – to become an explorer-naturalist, scientist, and to think like 'Sherlock Holms' and to act like 'Tintin'! Each of the below mentioned acknowledgements should be considered an understatement, each of which represents lasting memories, and friendships remembered well.

My graduate advisor Dr. Ian Jones should get the highest credit. Without his sincere faith in my abilities, and generous research support, this project would not have materialized. His easygoing approach as a supervisor, deep knowledge on ecology and natural history, and keen interest in science had helped synthesizing this dissertation. I will cherish the stimulating discussions that I had with him on topics ranging from evolutionary ecology and animal behaviour, identification of rare birds (in many of our birding trips), to world politics - he has been much more than just a supervisor: a mentor and a guide. Dr Ted Miller is in my supervisory committee but became almost a co-supervisor. I enjoyed his critical comments, stimulating discussions drawing on his experience with ethology, and most of all his bitter (yet constructive) criticisms. He was instrumental in helping me to direct my thoughts especially in the vocal behaviour of alcids. Ian, Ted and Dr. Bill Montevecchi, the third member of my supervisory committee, have given me their fullest support; much needed encouragement, criticism of manuscripts and valuable ideas, throughout.

For their support I also thank Dr Steve Carr and Dr Dawn Marshall (allowed me to use their labs and advise on phylogenetic analyses), Dr. Dave Schneider and Dr. Keith Lewis (assisted me with statistics), Shirley Kenny and Staff of the Biology office, Dr Peter Scott, Dr. Tom Chapman, Dr. Kim Bell, Peter Earle, Roy Ficken, staff of the Biochemistry store, and staff of the QEII and Health Science libraries. The major funding for this four-year project was provided by Ian's research grants and the fellowship from the Gradate School. The Macaulay Library of Natural Sounds, Cornell

Lab of Ornithology, provided research equipment and technical support for the auklet vocal recordings. For that I am thankful to Greg Budney and Mike Anderson. American Museum of Natural History (Frank M. Chapman Memorial Grant) and American Ornithologist's Union (Donald L. Bleitz Research Award) funded the auklet mechanosensory ornament study.

I was 'baptized' as a field biologist during the summers that I spent in the Aleutian Islands. However, Alaskan fieldwork demanded a great deal of courage, anxiety and stress, yet has remained as the nicest experience of this whole project. Thanks to a number of people, fieldwork was conducted with great ease. In the Alaska Maritime National Wildlife Refuge (AMNWR) of the U.S. Fish and Wildlife Service, Jeff Williams, Vernon Byrd, and Lisa Scauff greatly assisted me with logistics, permits and other field necessities. My hard working, enthusiastic field assistants; Grant Humphries, Chris Small, Pam Woodman and Adam Hunt gave their maximum support in the field. Most of the fieldwork was done at night, in extremely wet and potentially dangerous terrain. Without their support I would not be able to finish this project in time. Further, I thank all the crewmembers of Aleutian field camps, who shared so many lasting memories especially at the Buldir cabin, in our 'little blue boat' and at the Adak bunkhouse. The late Captain Kevin Bell and his smart, skillful crew of M/V Tiglax (AMNWR research vessel) gave their fullest support in my sea voyages along the Aleutian chain. Deckhands Dan and John's boating skills were essential for night Whiskered Auklet capture efforts at Ulak and Davidoff Islands. Bobby the ship's cook always gave me the last minute camp essentials.

My colleagues at the ACWERN/SERG Lab in St. John's were a diverse set of friends who shared past several years of my life, assisted me to develop essential research skills, and provided the critical discussions. Especially Sabir Muzaffar has been an inspiration. I am extending my sincere gratitude to all of them; Alain Lusignan, Alex Bond, Cari Eggleston, Greg McClellend, Heather Major, Jenn Lavers, Johanne Dussureault, Rosana Parades, Stephanie Royston, and Stephan Lorenz. Good friends Chandrika *akka*, Manju Wijekoon, Janaka Elangage, Eranda Harinath, Dilan Amarasighe,

Terrence Madujith, Neel Chandrasekara, Eranda Jayatunga, Paul Jones, Paul Regular, Cristal Lenky, Michelle Wille and Kantha Chechi, assisted, encouraged and provided welcome company throughout.

My dear father, who himself is a birder and a keen naturalist, my mother with her strong fighting spirit, and my caring brother Hemantha share the credit for large potion of this study. From them I learned the basics of ornithology and ecology at our tea estate in Galle, Sri Lanka. Finally Charitha has been with me and shares all the wonders of our Canadian living. She has not only been the proofreader for my manuscripts and chapters, but also been my best friend and loving wife, who very patiently and understandingly beard the hardships of my long absence from home due to Alaskan fieldwork.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Some likely explanations for vocal divergence in Aethiini. A) The effect of breeding substrate; vegetated soft soil (solid line) and rock crevices (broken line), B) the effect of ornament expression; highly ornamented (dotted line), ornamented (broken line) and sparsely ornamented (solid line), C) colony attendance behavior; nocturnal (dotted line) and diurnal (solid line).

LIST OF APPENDICES

CO AUTHORSHIP STATEMENT

The conceptual framework of this dissertation, and the ideas presented here are my own. However, several experts have contributed towards the quality of this dissertation by providing critical comments. Besides the introduction (Chapter One) and the summary (Chapter Six), all the chapters are co-authored by my graduate advisor Ian L. Jones. Dr Jones provided the major research funding and contributed to the conceptual outline, study design and the presentation of the results in each of the four chapters. Edward H. Miller contributed his expertise on avian acoustics to Chapters Three and Five. His contribution to Chapter Three is significant in the support for vocal recordings, comments on the analysis and presentation of data. Steve M. Carr recompiled the molecular data and constructed the molecular phylogeny of Aethiini for Chapter Five. Furthermore Dr. Carr helped to formulate the conceptual framework and provided his expertise on phylogenetics to interpret results in Chapter Five. Below, I have listed the publications and the authorship arising from this dissertation.

Seneviratne S. S. and Jones I. L. 2008. Mechanosensory function for facial ornamentation in the Whiskered Auklet, a crevice dwelling seabird. Behavioural Ecology 19:784-790.

Seneviratne S. S. and Jones I. L. The origin and maintenance of mechanosensory feather ornaments. (manuscript is ready to be submitted to Auk).

Seneviratne S. S., Jones I. L. and Miller E. H. 2008. The vocal repertoires of auklets (Alcidae: Aethiini): structural organization and categorization (in revision - Wilson Journal of Ornithology).

Seneviratne S. S., Jones I. L., Miller E. H. and Carr S. M., Evolution of vocalizations and the vocal apparatus of auklets. (manuscript submitted to Evolution).

CHAPTER ONE

INTRODUCTION AND OVERVIEW

1.1. RATIONALE

Ornamentation in animals can be explained by several non-exclusive factors: because of their phylogenetic heritage, adaptations to the physical environment, or adaptations to their social environment (Westoby et al. 1995). The primary goal of this dissertation was to elucidate the roles of different selection pressures on evolution of ornamental traits in a group of seabirds (Alcidae, Aethiini) in relation to ornamental function and variability. Results of this study focused chiefly on vocalizations and ornamental feathers. In addition, my results lead to a new hypothesis for trait exaggeration and provide the first comparative descriptions of acoustic behaviour in the Alcidae. In this first chapter, I provide a conceptual outline for the dissertation, followed by an overview of biology of Aethiini (auklets), and summaries of other chapters.

1.2. FACTORS THAT CONTRIBUTE TO TRAIT EXAGGERATION

1.2.1. Sexual selection

Sexual selection has been the primary explanation for the evolution of elaborate ornamental traits (Darwin 1871, Andersson 1994, Amundsen 2000). As opposed to natural selection, where driving force is the struggle for existence, sexual selection explains the struggle for reproduction and in particular mating success (Darwin 1859, 1871, Anderson 1994). Intra-sexual competition for mates and (inter-sexual) mate choice are the major mechanisms of sexual selection, though, other mechanisms occur (Huxley 1938, Andersson 1994, Andersson and Iwasa

1996). Intrasexual competition favours traits that signal individual strength or status to improve success in physical combat or in 'psychological warfare' (Andersson 1994, Andersson and Iwasa 1996, Amundsen 2000). Mate choice is the process in which individuals of one sex choose a more agreeable member of the opposite sex for mating (Darwin 1871, Huxley 1938). Phenotypic traits and a suite of resources that can attract a potential mate at stake are commonly used as the basis of mate choice (Andersson 1994, Andersson and Iwasa 1996).

Traits associated with survival advantage and additive genetic variance can be selected through mate choice and later exaggerated beyond natural selection thresholds (Fisherian runaway process; Fisher 1958, Lande 1980, 1981, Kirkpatrick 1982). Alternately, individuals may be favoured by mating preferences evolved for reasons other than social interests (Sexual selection for sensory exploitation; Ryan et al. 1990, Kirkpatrick 1987). Such preexisting receiver biases to a particular trait (e.g., a shape or colour of an appendage) can establish new visual signals (Basolo 1990, Ryan 1990, Ryan and Rand 1993). Ornamental traits can be costly to produce and maintain (Andersson 1982a, b, Iwasa and Pomiankowski 1994, Emlen 2001, Kotiaho 2001, Pryke and Andersson 2005), hence the chooser can asses the quality of the presenter through the condition of these traits (Zahavi 1975, but see Balmford and Thomas 1992). The individuals with the most expressed 'handicap signal' may have the greatest survival skills (Maynard-Smith 1985), or only high quality males can invest on these handicaps (West-Ebarhard 1979). In certain situations, individuals can get

direct benefits (e.g. access to a particular resource) by choosing a mate, which can also be a decisive factor in mate choice (Anderson 1994).

Elaborate visual and acoustic signals may also have arose as species recognition and isolation mechanisms (Mayr 1963). In sympatry, selection favours divergence of species' recognizing signals as hybridization produces less viable offspring (Mayr 1963). Since vocal and plumage characters are among the major traits used for premating imprinting in birds, these same traits could have been used later as species recognition traits during mate choice (Price 1998). Therefore, sympatric species exhibit greater differences in ornamental traits than allopatric species in closely related species (Sibley 1957, West-Eberhard 1983, Kaneshiro 1988, Ryan and Rand 1993, Schluter 2000, Coyne and Orr 2004, Seddon 2005).

1.2.2. Natural selection

Phylogenetic history, and the social and physical environment can affect in various ways the process of trait elaboration through natural selection (Endler 1986). The signaling environment can alter the effectiveness of visual signals/ornaments (Burtt and Gatz 1982) through the general physical properties of the habitat (Endler 1992, 1993a, b, Endler et al. 2005). Animals thus have developed different strategies to increase the efficacy of visual signals (Hailman 1977, Bradbury & Vehrencamp 1998, Fleishman 2000). Similarly, environment can act on acoustic signals (Marten et al. 1977, Hunter and Krebs 1979, Wiley

and Richards 1982, Endler 1992, Tubaro and Segura 1995, Slabbekoorn and Smith 2002a, b, Slabbekoorn 2004, Boncoraglio and Saino 2007), mainly through signal interference from local ambient noise (Brenowitz 1982, Ryan and Brenowitz 1985, Slabbekoorn and Smith 2002b) and sound transmission properties of the local environment (Wiley and Richards 1982, Brown and Handford 2000, Slabbekoorn 2004). Both acoustic and visual signaling traits could have been subjected onto morphology, physiology and genotype of the sender (e.g., Jouventin 1982, Stearns 1989, Tubaro and Segura 1995, Fletcher and Tarnopolsky 1999, Podos 2001, Endler et al. 2005, Seddon 2005).

1.2.3. Selection tradeoffs between natural and sexual selection

The evolution of ornamental traits is governed through a balance of conflicting fitness advantages (Krebs and Davis 1991, Schluter et al. 1991) and studies of such opposing selection advantages are useful to elucidate mechanisms underlining the life history trade-offs (Schluter et al. 1991). Chenoweth et al. (2008) and Wilkinson (1987) pointed out that the sexual dimorphism in *Drosophila* fruit flies, for example, were increased by sexual selection but decreased through natural selection. Natural selection can affect dimorphism through ecological processes such as intersexual niche partition (Shine 1989), therefore, the natural selection pressure would act somewhat equally on both sexes (Shine 1989). However, sexual selection is generally considered to act unequally on different sexes and has traditionally been associated with

polygynous mating systems (Lande 1980, Preziosi and Fairbairn 1996, but see Jones and Hunter 1993). Hence, these unequal selection pressures can act upon traits variably, with respect to their spatial (Chenoweth et al. 2008) and temporal distribution (different life history stages; Schluter et al. 1991, Post et al. 1999). Similar opposing selection patterns have been demonstrated in birds. For example, long beaks favour greater winter survival in Song Sparrows (*Melospiza melodia*) and short beaks favour reproductive success (Schluter and Smith 1986).

Fitness compromise (cost) due to the expression of ornamental traits would be the primary reason for natural selection to act against the sexually selected ornaments (Kotiaho 2001). In *Drosophila,* the evolution of some of the chemical signals (pheromones) has been in part limited by the cost associated with the development of several other ornamental traits (Skroblin and Blows 2006). The challenge for the study of such confounding (opposing) selection pressures is that one selection force can mask the effect of the other (Schluter et al. 1991), and the effect could even be vary spatiotemporaly (Schluter and Smith 1986, Gibbs and Grant 1987, Stearns et al. 1991, Post et al. 1999). Further, these opposing selection forces are not always mutually exclusive (Westoby et al. 1995). Experimental manipulation of traits is an approach that can reduce this problem (Schluter et al. 1991), a strategy I employed in my study of feather ornaments (Chapters Two and Four).

1.3. ORNAMENTAL TRAITS IN COMPARATIVE CONTEXT

The evolutionary patterns of phenotypic traits can be tested through a comparative approach (Gittleman and Luh 1992, Lanyon 1992, Ryan 1996), where behavioural patterns of extant species have been used to determine similar patterns of others, and to understand relationships between species (e.g., Darwin 1859, Tinbergen 1959, Huxley 1966, Lorenz 1970, 1971, Harvey and Pagel 1991). Atz (1970), Frumhoff and Reeve (1994), Westoby et al. (1995), Price (1997), Omland and Lanyon (2000) and Masters (2007) pointed out some drawbacks of the use of behaviour in phylogenetic context, however, the comparative method has been developed as a valuable tool in behavioral ecology (Wenzel 1992, Burns 1998, Slabbekoorn et al. 1999, Martins 2000, Price and Lanyon 2002, Päckert et al. 2003, Kort and ten Cate 2004). In light of phylogenetics, comparative studies can be used to determine ancestral behavioural patterns, to infer mechanisms of evolution, the direction and magnitude of change, and other evolutionary processes such as speciation and random genetic drift (Martins 1996). However, the quality of the available phylogeny and the ability to adopt a quantitative approach could influence the quality of such studies (Gittleman and Luh 1992, Ryan 1996). The use of phylogenetics in a statistical context has been limited mainly due to the tendency of phylogenetic data being dependent on each other as the result of common ancestry (Harvey and Pagel 1991, Ridley and Grafen 1996). Reliance on parsimony in phylogetic reconstructions is another potential drawback (Ryan 1996). However, Felsenstein (1985), Harvey and Pagel (1991),

Gittleman and Luh (1992) and Møller and Birkhead (1992) provide tools to avoid some of these drawbacks.

Comparative method can take one of two approaches, (1) infering affinities based on a few presumably homologous traits (Davis 1962, Omland 1994, Johnson 1999, Omland and Lanyon 2000), or (2) using fairly large datasets to determine statistical relationships between characters (Harvey and Pagel 1991, Gittleman and Luh 1992, Møller and Birkhead 1992, Höglund and Sillén-Tullberg 1994). In this dissertation I have used both these approaches in addition to an experimental approach.

1.4. THE STUDY GROUP: ALCIDAE (AVES: CHARADRIIFORMES)

The Alcidae is a group of seabirds consisting of 23 extant species (Gaston and Jones 1998). It is the only group of birds specialized in a wing-propelled diving niche in the Northern Hemisphere (Bédard 1967), a niche occupied by diving petrels (Pelecanoididae) and penguins (Spheniscidae) in the southern oceans. Most species breed on remote oceanic islands devoid of land predators, or on cliff ledges inaccessible to such predators. Outside the breeding season most of them disperse in the open ocean away from any landmass (Gaston and Jones 1998).

The Alcidae originated in the eastern North Pacific ~60 Mya after diverging from the lineage leading to skuas and jaegers (*Skua* and *Stercorarius*: Pereira and Baker 2008). Two major clades are present in the family; the puffins and auklets (Fraterculini and Aethiini), and the picivorous murres, murrelets and

guillemots (Alcini, Cephini, Brachyramphini and Synthliboramphini; Strauch 1985, Friesen et al. 1996, Gaston and Jones 1998, Pereira and Baker 2008; Figure 1.1). The basic relationships within the family, and many species-level relationships within clades, have been well established through morphological and molecular studies (Strauch 1985, Watada et al. 1987, Friesen et al. 1996, Moum et al. 1994, 2002, Thomas et al. 2002a, b, Baker et al. 2007, Pereira and Baker 2008).

Within the order Charadriiformes, Alcidae express a very frequent occurrence of visual ornamentation, ranging from exaggerated feather crests and bright red beaks to contrasting colour patches in the plumage (Gaston and Jones 1998). All members of the Fraterculini-Aethiini clade, except Cassin's auklet, express conspicuous visual ornaments. However in the sister clade, only Japanese (*Synthliboramphus wumizusume*) and Ancient Murrelets (*S. antiquus*) have distinctive ornamental feathers (Gaston and Jones 1998). Except for the Fraterculini, all alcids are highly vocal at their breeding colonies (Gaston and Jones 1998).

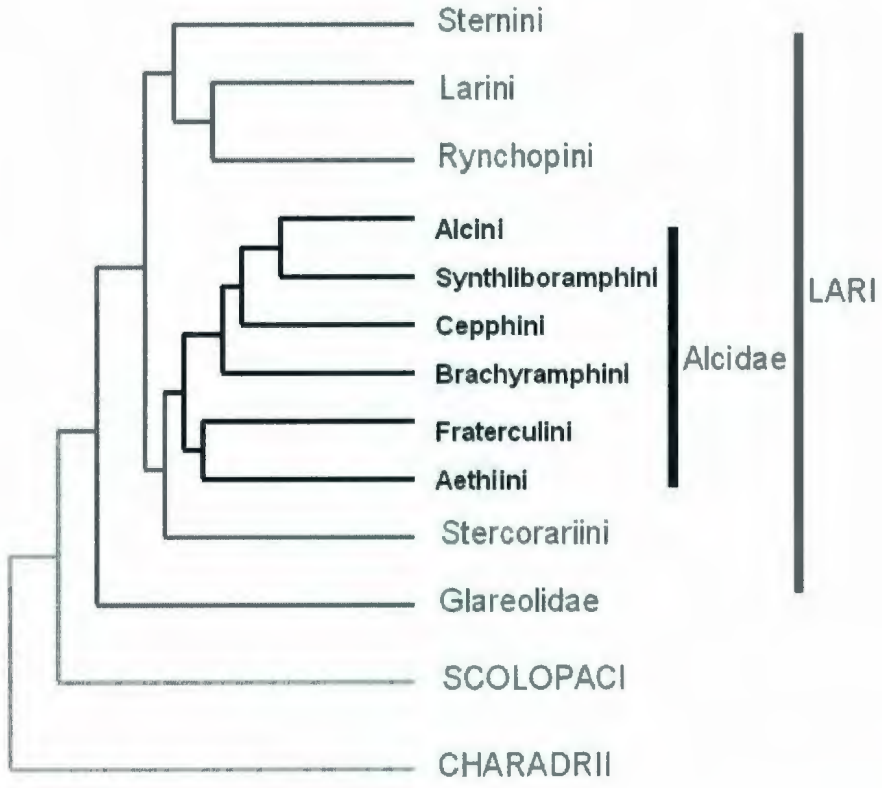

Figure 1.1

The family and subfamily level relationships of the suborder Lari (after Baker et al. 2007), and the relationships of the six tribes of Alcidae (after Pereira and Baker 2008). The relative position of major clades (Lari, Scolopaci and Charadrii) in Charadriiformes is also shown.

1.4.1. True auklets (Tribe Aethiini)

Aethiini is a monophyletic clade of five extant species that inhabit the North Pacific (Figures 1.2 -1.4): Cassin's Auklet (*Ptychoramphus aleuticus*), Crested Auklet (*Aethia cristatella*), Least Auklet (*A. pusilla*), Parakeet Auklet (*A. psittacula*), and Whiskered Auklet (*A. pygmaea*) (Gaston and Jones 1998). The tribe diverged from its sister group (puffins) ~50 Mya and *Ptychoramphus* diverged from *Aethia* ~20 Mya (Pereira and Baker 2008). Previous phylogenetic hypotheses were unable to resolve affinities within the members of Aethiini (Strauch 1985, Watada et al. 1987, Moum et al. 1994, Friesen et al. 1996, Thomas et al. 2004, Walsh et al. 2005, Pereira and Baker 2008; Figure 1.2), however, all those phylogenies agreed that within the tribe the Cassin's auklet is basal to the remaining species, which, therefore makes *Aethia* a monophyletic genus.

Plumage traits of auklets that are specialized for intraspecific visual communication include conspicuous silvery-white facial plumes (four species) and forward-curved forehead crests (two species; Gaston and Jones 1998, Jones 1999; Figure 1.3). Experimental evidence indicated that Crested Auklet's crests are favored by both intra- and intersexual selection (Jones and Hunter 1993, 1999). Closely related, crestless Least Auklets (*A. pusilla*) have similar mating

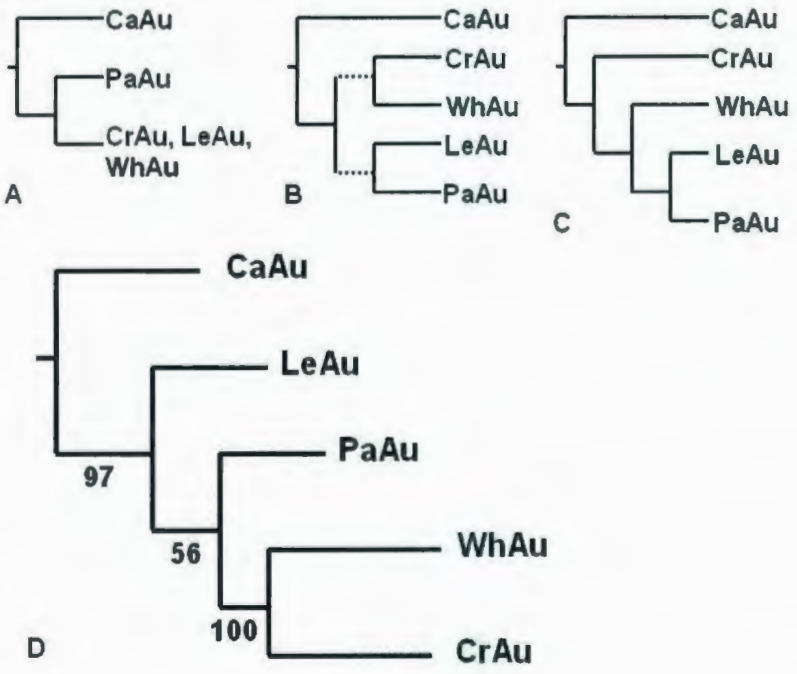

Figure 1.2

Alternative phylogenetic hypotheses for Aethiini based on (A) morphology (Strauch 1985), (B) mitochondrial DNA and allozymes (Freisen et al. 1996), (C) a supertree approach (Thomas et al. 2004b) and (D) recent analysis of mitochondrial DNA and allozymes (Pereira and Baker 2008). Numbers at nodes indicate bootstrap support, and broken lines indicate poorly supported branches. Abbreviations for the species are; CaAu, Cassin's Auklet; CrAu, Crested Auklet; LeAu, Least Auklet; PaAu, Parakeet Auklet; WhAu, Whiskered Auklet.

Figure 1.3

The elaborate facial feathers and bill plates of breeding plumage adult Aethiini auklets. (A) Cassin's Auklet, (B) Least Auklet, (C) Parakeet Auklet, (D) Whiskered Auklet, and (E) Crested Auklet.

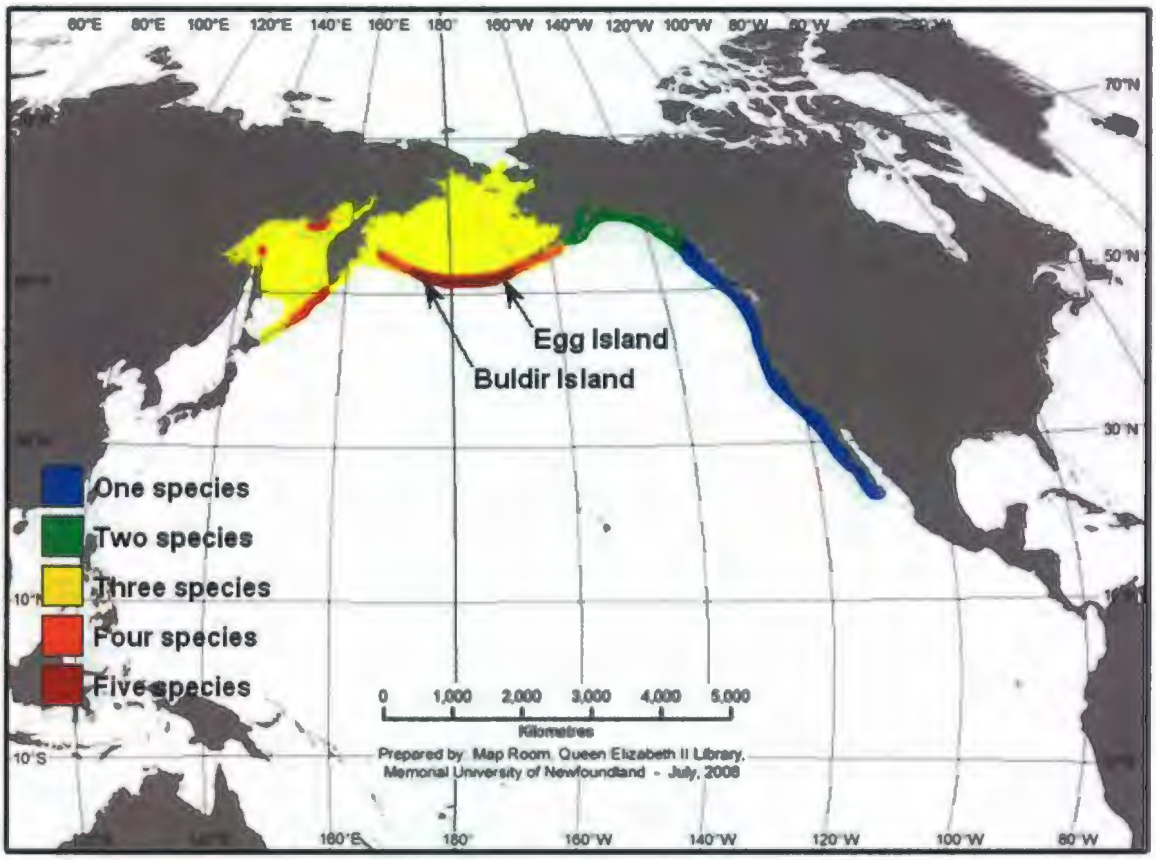

Figure 1.4

The geographic distribution (breeding range) of Aethiini auklets in the North Pacific (after Jones 1999). The two main study sites in the Aleutian Islands (Buldir and Egg Islands) are also indicated.

preferences for their white facial plumes and red bill colour (Jones and Montgomerie 1992), and for an experimentally attached Crested Auklet crest (Jones and Hunter 1998).

The Whiskered Auklet possesses a slender forehead crest and several sets of antenna-like white facial plumes; these include superorbital plumes that extend above the eye over the crown from either side of the head, suborbital plumes that extend along the neck and auricular plumes that extend from below the eye towards the neck (Gaston and Jones 1998; Pitocchelli et al. 2003; Figure 1.3). The white facial plumes are elongated filoplumes; the forehead crest consists of elongated contour feathers (Konyukhov 2001). Whiskered Auklets are active on land at their breeding colonies only at night, and most displays given on land occur within rock crevices, hampering attempts to experimentally investigate ornament function. However, the display of Whiskered Auklet's crest and plumes during social activity (Hunter and Jones 1999; Zubakin and Konyukhov 1999, 2001), have suggested that the Whiskered Auklet's ornaments might be a similar product of mutual sexual selection (Jones 1999). Crested Auklets display the forehead crest and orange coloured bill plates (Figure 1.3) only in the breeding season (Jones 1993a). The Least Auklet has a beak knob made out of similar plates, and a patch of slightly extended white plumes (Jones and Montgomerie 1991, 1992; Figure 1.3). The Parakeet Auklet has a distinctive red parrot-like bill partly evolved as an adaptation to its specialized foraging niche (Gaston and Jones 1998, Jones et al. 2001; Figure 1.3). All members of the genus *Aethia* show

auricular plumes (see above; Figure 1.3). The Cassin's Auklet does not display any conspicuous plumage traits, however, it shows crescent-shaped white patches above and below the eye in all plumages (Manuwal and Thoresen 1993).

Auklets are highly vocal at their breeding colonies and general information about their vocal repertoires is available (Manuwal and Thoresen 1993, Jones 1993a, b, Byrd and Williams 1993, Jones et al. 2001). Mixed-species auklet colonies are nearly universal, however, they inhabit acoustically variable habitats along their breeding range (coastal cliffs, talus and lava flows, hillsides with varying amounts of grass cover; Jones 1993a, b, Manuwal and Thoresen 1993, Gaston and Jones 1998, Jones 1999, Jones et al. 2001). Consequently, divergent adaptations to differing physical environments are possible.

The social environments of auklet species are similar: they are colonial and socially monogamous. *Aethia* show intense social activities at sea in groups (rafts) near their colonies (Hunter and Jones 1999), which are absent in *Ptychoramphus* (Thoresen 1964). Colony attendance behavior of the members is variable as well; Cassin's and Whiskered Auklets visit the colony at night, the remaining species are diurnal (Gaston and Jones 1998). The breeding habitat for auklets are slightly variable as well: Cassin's Auklets breed exclusively in soft soil in slopes covered with grass and even sometimes trees that facilitates its burrow excavation (Thoresen 1964, Manuwal and Thoresen 1993), Crested and Least Auklets breed exclusively in natural rock crevices (Jones 1993a, b), Whiskered Auklets prefer such rock crevices but also uses soil and grassy slopes

embedded with rocks (Zubakin and Konyukhov 1999, Hunter et al. 2002; Seneviratne unpublished data). The Parakeet Auklet breeds in rock crevices, natural cavities in soil, and self excavated burrows (Jones et al. 2001).

1.5. JUSTIFICATION FOR THE SPECIES USED

Auklets were chosen to investigate the adaptive significance of ornamental and vocal traits for several reasons. The group is monophyletic, and falls within a well-resolved clade (Paton et al. 2003, Thomas et al. 2004a,b, Paton and Baker 2006, Livezey and Zusi 2007, Pereira and Baker 2008, Figure 1.1). Auklets are the product of an explosive adaptive radiation that produced a wide variety of ornamental traits (Jones 1999). Within the tribe, the genus *Ptychorhamphus* is sister to *Aethia* (Strauch 1985, Friesen et al. 1996, Moum et al. 1994, 2002, Jones 1999, Thomas et al. 2004a, b, Pereira and Baker 2008), which therefore makes *Aethia* a monophyletic genus (Figure 1.2). In the breeding season they are highly ornamented and are very vocal. Further all these auklets share similar social and physical environment in their sympatric Alaskan breeding colonies (Gaston and Jones 1998, Jones 1999; Figure 1.4). Finally, several aspects of their behavioral ecology have been fairly well studied in the past several decades (e.g. Bédard 1969, Strauch 1985, Jones and Hunter 1993, Friesen et al. 1996, Gaston and Jones 1998, Konyukhov 2001), which have established background knowledge of the behaviour and phylogeny for this dissertation.

1.6. OVERVIEW OF THE CHAPTERS

The primary objective of this study was to understand the role of different selection pressures on the origin and maintenance of some of the ornamental and vocal traits in auklets. The function and variability of several visual and acoustic traits were used to achieve this objective. I investigated the variability and function of elongated facial plumes, mainly the forehead crest and the vocalization of adults at the breeding colony, which is described in Chapters Two and Three. These preliminary descriptions provide the baseline for a comparative study to elucidate the phylogenetic and ecological significance of these ornamental traits (Chapters Four and Five). Hence, in addition to revealing the role of different selection forces in vocalization and some of the ornamental feather traits, this dissertation empirically tests a novel hypothesis for plumage exaggeration and provides a quantitative baseline for vocal repertoire of the entire clade, and is the first such vocal analysis for any group within Alcidae.

In Chapter Two (Mechanosensory function for facial ornamentation in the Whiskered Auklet, a crevice-dwelling seabird), I experimentally measured Whiskered Auklets' ability to avoid obstacles in the absence of visual clues in a darkened maze, with and without the assistance of the forehead crest and superorbital plumes. The objective was to test whether the feather ornaments are used as a mechanosensory device to avoid obstacles during their nocturnal underground navigation in the absence of visual clues. I predicted that if Whiskered Auklets' elongated plumage ornaments have a mechanosensory role,

the subjects would have a greater difficulty in navigation under the absence of these traits.

The main objective of Chapter Three (Vocal repertoires of auklets: structural organization and categorization) is to characterize the structural organization of vocal repertoires of the five extant auklet species. I conducted a comprehensive description of auklet vocalization to elucidate vocal relationships in Aethiini. I hypothesized that if *Ptychoramphus* (Cassin's Auklet) is the sister group to *Aethia*, as suggested in molecular and morphological phylogenies, this would be reflected in the pattern of ancestral and derived vocal traits. The alternate hypothesis was that ecological and social differences could cause vocal divergence.

In Chapter Four (Origin and maintenance of mechanosensory ornaments in birds), I have tested comparatively the mechanosensory ability of auklet crest ornament using Crested and Least Auklets in a lightproof maze. The hypothesis was that if Whiskered Auklet's mechanosensory ability has been enforced by the environment, the Crested Auklet that shares a similar phylogenetic past and breeding habitat should have the same tactile use for its crest. The crestless Least Auklet was the control for this comparison. Then a pairwise comparison (controlled for phylogeny) across all non-passerine bird families was carried out to test if there is a correlation between the habitat complexity and the expression of such facial ornaments. I predicted that if environment plays a major role in triggering mechanosensory facial plumes, the elongated facial plumes would be

more likely to be expressed in birds that live in complex habitats and lowlight conditions.

In Chapter Five (Evolution of vocalizations and the vocal apparatus of auklets), I used acoustic characters from total repertoires along with some syringeal characters to identify correlates with vocal divergence. I hypothesized that phylogenetic relationships among auklets would play the greatest role in determining vocal divergence. Hence I predicted that the vocalization of closely related Crested and Whiskered Auklets would be more similar to each other than those of Least and Cassin's Auklets, and the vocalization of *Aethia,* in general, would be different to that of its sister species. It was further anticipated that this comparison would provide insight into the selective forces that have driven species divergence in Aethiini.

The last chapter (Chapter Six: the summary) provides an overall discussion for the dissertation, including my major conclusions and suggestions for future research.

CHAPTER TWO

MECHANOSENSORY FUNCTION FOR FACIAL ORNAMENTATION IN THE WHISKERED AUKLET, A CREVICE-DWELLING SEABIRD

2.1. ABSTRACT

Sexual selection has been the prevalent explanation for the evolution of birds' elaborate feather ornaments. An overlooked possibility is that feather appendages arose due to a naturally selected sensory function involving sensitivity to pressure or touch to facilitate obstacle avoidance either in flight or on land. Here I show experimentally that elongated facial feather adornments of Whiskered Auklets (*Aethia pygmaea*), a sexually monomorphic crevice dwelling seabird, have a mechanosensory use for orientation in darkness underground. While navigating inside a lightproof maze simulating the structure and conditions of breeding crevices, Whiskered Auklets (n = 99) showed a 275% increase in frequency of head bumps in the absence of their protruding feather crest and facial plumes. A weak positive relationship ($R = 0.36$, $p = 0.04$) between natural crest length and the frequency of head bumps in the absence of the crest suggested that individuals with longer ornaments depend more on these traits for navigation in the wild. I hypothesize that protruding feathers evolved through a combination of natural selection for sensory function and sexual selection as known for other auklets. More widely, birds inhabiting cluttered environments would benefit from elongated facial plumage that mechanically detects obstacles.

2.2. INTRODUCTION

Sexual selection driven by mating preferences has been a common explanation for the evolution of feather adornments such as showy tails, bright plumage coloration and crests in birds (Darwin 1871; Andersson 1994). Such ornamental traits may be favored during mate choice because of an arbitrary genetic linkage between trait and preference (Fisher 1958; Kirkpatrick 1982; Kirkpatrick and Ryan 1991), because they indicate health or viability (Hamilton and Zuk 1982; Andersson 1986), or because they exploit sensory biases of the chooser (Basolo 1990; Ryan 1990). Some evidence does not support a sexually-selected function for such feather ornaments e.g.: involvement of composite traits, hence inability to detect a weak preference (Johnstone 1996; Hagelin and Ligon 2001); secondary transformation of the original function (Ligon and Zwartjes 1995; Wiens 2001; Parker et al. 2005); and development or maintenance of traits by non-sexual selection. Other functions for elaborate feather traits have been suggested, including camouflage and predator evasion (Baker and Parker 1979), individual recognition (Whitfield 1987, Dale 2000), fertilization success (Birkhead and Møller 1992), aerodynamic performance (Rowe et al. 2001, Bro-Jørgensen et al. 2007) as a feeding apparatus (Jackson 2003), and as a protective guard (Conover and Miller 1980). An additional, neglected, possibility is that elaborate feather appendages could serve a sensory function either in flight (to aid in optimizing aerodynamic performance) or on the ground, to facilitate obstacle avoidance in a complex environment.

Bird feathers are complex integumentary derivatives with varied functions (Lucas and Stettenheim 1972; Spearman and Hardy 1985; Clark 2004). Filoplumes are hair-like feathers with a fine shaft and sparse barbules, which together transmit vibrations and pressure changes to sensory corpuscles (Stettenheim 1972; Gottschaldt 1985). Filoplumes serve as mechanoreceptors within the plumage for aiding flight and general plumage maintenance (Lucas and Stettenheim 1972; Spearman and Hardy 1985; Brown and Fedde 1993; Clark 2004). Filoplumes visibly project beyond the surrounding contour feathers in several orders: Pelecaniformes (Childress and Bennun 2002); Procellariformes (James 1986); and Passeriformes (Clark and Cruz 1989). Such elongated filoplumes in some passerines may aid in feather self-maintenance in parts of the plumage that are not visible to the bird (Clark and Cruz 1989). Some filoplumes form ornate external structures that might have a role in display. For example, the elongated filoplume-crest of the Great Cormorant (*Phalacrocorax carbo*) is a condition-dependent signal used in mate assessment (Childress and Bennun 2002) with untested sensory use. However, most feather ornaments are modified contour feathers, flight feathers or rectrices (Andersson 1994). Bristles (another feather type) are found primarily on the head, and are associated with numerous sensory receptors (Küster 1905; Schildmacher 1931; Lucas and Stettenheim 1972). Facial bristles occur in several unrelated avian families that are either nocturnal or crepuscular, breed in tree cavities, or feed on flying insects (e.g. Caprimulgidae, Mimidae, Capitonidae and Tyrannidae). Küster (1905) and Lucas

and Stettenheim (1972) suggested that these structures could be used as tactile organs, analogous to mammalian vibrissae, to negotiate cluttered or low-light situations, however, this hypothesis has not been investigated (Lederer 1972; Conover and Miller 1980; Jackson 2003).

Whiskered Auklets (*A. pygmaea*) are the most facially ornate auklet species, possessing a slender black forehead crest and three tracts of antenna-like silvery-white elongated facial plumes (Gaston and Jones 1998; Pitocchelli et al. 2003; Figure 2.1). Detailed anatomical study demonstrated previously that the white facial plumes are elongated filoplumes; the forehead crest comprises elongated contour feathers (Konyukhov 2001). I measured experimentally the ability of Whiskered Auklets to avoid obstacles in a darkened maze, which is similar to conditions in breeding crevices at night where the colony activity takes place, with and without the assistance of elongated facial plumes. My objective was to test whether the ornaments of Whiskered Auklets are used as a sensory device to avoid obstacles during nocturnal underground navigation. Exploratory behavior of the subjects was recorded under near-infrared illumination. I predicted that if the ornaments have a sensory role, the subjects would bump their head against the maze walls and roof more frequently when crest and superorbital plumes were inactivated.

Figure 2.1

Adult Whiskered Auklet (*Aethia pygmaea*) showing the forehead crest and white facial feather ornaments.

2.3. METHODS

Fieldwork that included capturing auklets, exposing them to the test chamber and taking measurements, was undertaken at Buldir Island, western Aleutian Islands, Alaska, USA (52°22'N, 175°54'E) in May to July 2006. Experimental trials were conducted during the incubation phase of the breeding season, as the expression of feather ornaments declines later due to molt (Konyukhov 2001). Birds were captured using two 12 m mist nets at night (0030-0530 h; Aleutian standard time) similar to the method of Jones et al. (2007) at six locations in ~1 km long beach (North Bight; Byrd and Day 1986). I believe that the nets captured birds more-or-less randomly (Jones et al. 2007). Captured birds were held temporarily in separate ventilated cloth bags for processing and exposed to a light-tight chamber (maze) to test exploratory behavior under different treatment conditions.

2.3.1. Experimental setup - test maze

A three-chambered wooden box (Figure 2.2) simulating a natural breeding crevice was used as a maze to test birds' ability to avoid obstacles in the absence of visual clues. The maze consisted of three wooden chambers. The lightproof test chamber was 10 (height) x 35 x 30 cm in size, with ventilation holes and two sidewalls to prevent birds from moving away from the field of view of the camera. Two 2 x 8 x 8 cm wooden panels were attached to the roof as barriers, which the birds were required to avoid. The entranceway (10 x 10 x 10 cm)

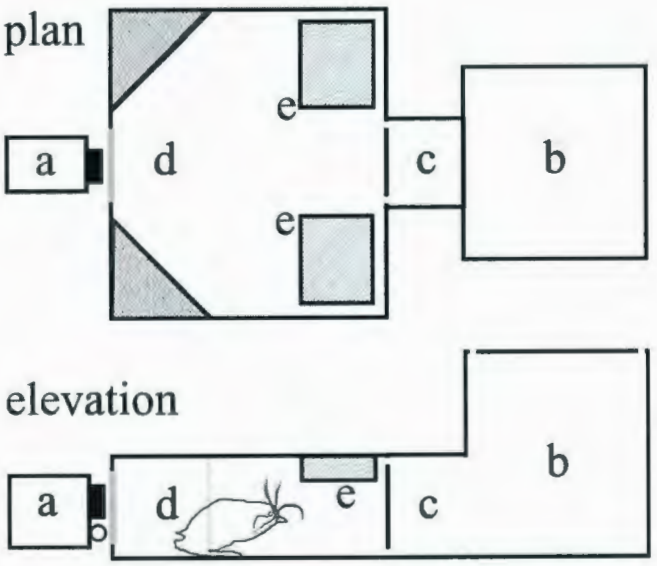

Figure 2.2

Setup of the Whiskered Auklet experimental maze with (a) digital camera with the light source, (b) test chamber, (c) entrance way to the test chamber, (d) holding pen and (e) the barriers attached to the roof of the test chamber.

connected the 20 x 20 x 20 cm holding pen to the test chamber. The floor consisted of rough cardboard to allow birds to walk as in their natural crevices (Hunter et al. 2002). To avoid light penetration, the inside and outside of the boxes were painted flat black, the entire maze was covered with a thick black cloth, and the experiment was carried out in darkness at night. A digital camcorder (Samsung SCD103) with built-in infrared light-emitting diode (peak wavelength 880 nm, part number 0601-001626) recorded behavior through a 7 x 4 cm opening in the front wall of the test chamber (Figure 2.2). I used the camcorder's 'Nite pix' mode (Samsung Owner's Instructions), which allowed recording under near-infrared illumination with a greater sensitivity to the longer wavelengths (peak spectral sensitivity ~700-800 nm). Peak spectral sensitivity of birds in general falls between 350-600 nm (Hart 2001). Specific information on auklet visual perception is lacking, but spectral sensitivity of phylogenetically (gulls; Liebman 1972) and ecologically (shearwaters and penguins: Bowmaker and Martin 1985; Bowmaker et al. 1997) related bird groups is restricted to this range (Hart 2001). Therefore I assumed that auklet vision was insensitive to infrared wavelengths emitted by the Samsung SCD103, and that my subjects had no visual clues to navigate inside the maze. Due to their flexibility and narrow width (less than 1 mm), crest and superorbital plumes did not produce enough pressure for us to consistently measure the number of touches using a trial remote detection system using touch or pressure detectors (field trials during June 2005).

The alternate camera-based visual scoring system was portable and withstood severe weather conditions in the field. Therefore, I was able to increase my sample size and decrease overall stress for the birds by conducting the experiment in a permanent blind situated close to the breeding colony at night during the times of peak colony activity.

2.3.2. Treatment exposure procedure

Each bird (n = 99) was exposed to three treatments in a balanced random order: ornament manipulation, control and sham. In the ornament manipulation treatment, the forehead crest and superorbital plumes were taped to the back of the head using three pieces of 8 x 2 mm black one-sided tape. The tape was attached to the nape of the subject, causing these plume tracts to blend smoothly with the rest of the crown feathers. The forward-projecting crest and the superorbital plumes are thin, highly flexible feather ornaments (Figure 2.1) that are bent and lay flat with the crown and facial feathers in flight and during underwater diving in the wild (Byrd and Williams 1993; Gaston and Jones 1998; and S.S. and I.L.J. personal observations). Because it mimics the natural movement for these feathers, my experimental manipulation (bending these extremely flexible feathers) was unlikely to cause unusual stress to the ornament or cause pain or irritation to the bird other than the distraction caused by the small pieces of tape attached. A sham treatment was used to test for the effect of taping: three 8 x 2 mm pieces of tape were attached to the nape similar to the

manipulative treatment but without altering crest or superorbital plumes. The test bird was introduced to the maze unmodified (no ornament alteration) in the control treatment. I manipulated only the crest and superorbital plumes, because they extend above and to the sides of the head (Figure 2.1), and their contacts with maze walls and ceiling were clearly detectable (Figure 2.2). Preparation of the bird for each treatment took less than a minute and each bird (99) was subjected to all the above treatments once, in a sequential (constrained random) order in all possible combinations; MCS, MSC, CMS, CSM, SMC, SCM (with M = manipulation, C = control, S = sham), e.g., bird n_1 was exposed to MCS, n_2 to MSC etc. Hence 34 birds were exposed initially to C, 33 to M and 33 to S. The order of the exposure of subsequent treatments (second and third exposures; see above) was chosen in a constrained random order to reduce the carryover effect due to repeated exposure (Neter et al. 1996).

Birds were placed initially in the holding pen for several minutes to acclimate and were permitted to walk from the pen to the test chamber (Figure 2.2). After the bird entered the test chamber its exploratory behavior was video recorded for ~2 min. After each exposure, the subject was removed from the maze, switched to the next treatment and immediately replaced in the holding pen for the next treatment. Video recordings were uploaded to a computer. The definitions of unambiguous 'head bump', 'crest contact', 'superorbital plume contact' and 'beak contact' were defined prior to the counts. I did not count blindly to knowledge about the treatment, because to count these effects the

observer had to view the recordings, where the treatment manipulations were easily distinguishable. In the laboratory I reviewed the recordings and counted the frequency of head bumps (number of head touches on the roof and the walls per minute) crest contacts, superorbital plume contacts and beak contacts (similar to the other counts) in a dark room using tally counters. Following Zubakin and Konyukhov (1999), I observed birds' behavior in the colony throughout the breeding season using a dim red lithium electrode diode headlamp and the above camcorder with infrared light source.

2.3.3. Ornament measurements

After the experiment, birds were marked with plastic leg bands to avoid retesting them in the event of recapture, and their crest and superorbital plumes were measured using dial calipers (to ± 0.02 mm). Crest was measured from the base of the feathers to the tip of the longest feather, with the feathers flattened and straightened. Superorbital plume length was measured on both sides of the head, from the anterior-most point of origin of white plumes near the base of the bill, to the tip of the longest plume, with the plumes straightened and parallel. Only adults were used for the experiment. Subadults were identified by extensive pale brown contour feathering on their forehead, chin, neck, and by similarly worn secondaries and greater coverts (Konyukhov 2001; Pitocchelli et al. 2003). All birds were released near the original capture site within 30-120 min after their capture. As part of other work on Whiskered Auklets at Buldir Island, I. L. Jones

measured feather ornaments (as above) and also body mass (to ± 1 g), tarsus length, bill length, and bill depth (to ± 0.02 mm) for a large sample of adults captured each year during 1992-2006.

2.3.4. Analysis

I used Minitab Release 13.31 (Minitab Inc., State College, Pennsylvania, USA) and Statview (Caldarola et al. 1998). The cumulative effect of stress and the bird's habituation to the maze caused by repeated handling and exposure to different treatments, were collectively tested using the order of treatment exposure, which was tested using general linear model as two-way ANOVA by keeping both treatment (C, M, S) and order of exposure (C--, -C-, --C; M--, -M-, --M; S--, -S-, --S) fixed (Sokal and Rohlf 1995). Order of exposure on mean number of head bumps to the maze had no significant effect ($F_{2,8} = 3.52$, $p = 0.131$). However, because of the lower probability obtained, further analyses were performed to test the same effect in each of the three exposures separately using all 99 birds assigned randomly to the nine possible combinations. Each bird was used once to represent one of the treatments. One-way ANOVA (with Bonferroni correction) was used. No treatment showed a significant effect of order of exposure on frequency of head bumps. The frequency of head bumps for manipulation was: first exposure 3.31 (±0.57 SEM); second exposure 3.17 (±1.00); and third exposure 2.17 (±0.58); ($F_{2,35} = 0.46$, $p = 0.634$). Frequencies of head bumps for first, second and third exposures of the control were: 1.01

(±0.25), 0.86 (±0.25) and 0.76 (±0.19), respectively ($F_{2,31}$ = 0.29, p = 0.748); corresponding values for the sham were 1.60 (±0.38), 0.77 (±0.24), and 1.05 (±0.26); ($F_{2,24}$ = 1.71, p = 0.202). Hence I assumed that the level of stress or habituation caused by repeated exposure and handling was not significant enough to alter the results. The frequency of head bumps, beak contacts, total contacts, crest contacts, and facial plumage contacts under different experimental treatments were compared using two-way ANOVA with randomized blocks (Sokal and Rohlf 1995). Individual birds (n = 99), were the blocks, hence were treated as random, with treatment fixed. Residuals were checked for normality, homogeneity, and independent errors. There were no significant deviations of residuals from normality, and errors were homogenous and independent. Relationships between ornamental traits and contacts with the maze were tested using general linear model (regression; Sokal and Rohlf 1995). Statistical significance of all tests was reached at $\alpha = 0.05$.

This study was conducted under the approval of the Animal Care Committee of the Memorial University of Newfoundland (protocol numbers 06-13-IJ and 06-14-IJ). Throughout the study, recommendations of the Canadian Council on Animal Care (CCAC) and the Animal Behavior Society guidelines for the use of animals in research were followed.

2.4. RESULTS

Birds in the maze displayed similar behavior to that in their natural crevices in all three treatments. In the test maze my subjects showed a significantly greater frequency of head bumps in the crest and facial plumes taped-down (manipulative) treatment than in the control and sham-manipulated treatments (two-way ANOVA; Tables 2.1-2.2) with more than double the frequency of head bumps (275%) in the absence of the protruding feather traits (Figure 2.3). The difference in mean frequency of head bumps and feather ornament contacts between control and sham treatments did not significantly differ (Figure 2.3; Tables 2.1-2.2) suggesting that stress caused by attached tape did not cause these birds to bump into maze walls more often than unaltered birds. The frequency of contact of feather ornaments with the ceiling and walls of the maze was high in the control and sham birds (Table 2.1) and showed a significant reduction in frequency to near zero due to plumage manipulation (Figure 2.3; Table 2.2). For birds' first exposure to the maze (n = 33), I detected a positive relationship between natural crest length (mean crest length; 38.72 [± 7.32 SD] mm) and the frequency of head bumps in the manipulative treatment (Figure 2.4a; Tables 2.1-2.2), suggesting that birds with longer ornaments had greater difficulty navigating under the plumage manipulation. Birds with longer forehead crests also had longer superorbital plumes (mean average superorbital plume length, 32.75 [±5.85 SD] mm; Figure 2.4b; Table 2.2).

Table 2.1

Whiskered Auklet's ability to negotiate the experimental maze under different treatments. (a) to (d) all three exposures (first, second and third) combined; birds' first exposure to the maze, (e) in plumage manipulation treatment and (f) in control treatment (unmanipulated ornaments).

Variable	Mean	SEM	n	Variable	Mean	SEM	n
(a) Head bumps				**(d) Total hits**			
Manipulation	2.78	0.22	99	Manipulation	6.60	0.58	99
Control	1.01	0.12	99	Control	13.07	0.79	99
Sham	0.86	0.08	98	Sham	13.42	0.63	98
(b) FO hits				**(e) Manipulation**			
Manipulation[a]	-	-	-	Head bumps	3.07	0.28	32
Control	9.34	0.50	99	**(f) Control**			
Sham	9.98	0.46	98	Crest hits	7.74	0.70	33
(c) Beak hits				SOP hits	1.50	0.28	33
Manipulation	3.82	0.41	99	Total FO hits	9.24	0.78	33
Control	2.73	0.32	99	Beak hits	3.17	0.66	33
Sham	2.43	0.28	98	Total hits	13.56	1.43	33

SEM, standard error of mean; FO hits, total feather ornament hits with the maze; SOP hits, superorbital plume hits with the maze.

[a] The expression of feather ornaments was cancelled in manipulation (see methods).

Table 2.2

Comparison of the effect of different treatment exposures, and the relationship of feather ornament length with body size.

Variable	F	df	p	R^2
Head bumps under plumage manipulation	63.21	2,196	<0.001	
Head bumps between control and sham	1.14	1,98	0.288	
Ornament contacts between control and sham	2.04	1,98	0.156	
Ornament contacts in plumage manipulation	142.14	2,196	<0.0001	
Beak contacts under plumage manipulation	7.62	2,196	0.001	
Relationship with natural crest length				
Head bumps under plumage manipulation	4.45	1,30	0.043	0.13
Natural superorbital plume length	67.35	1,96	0.0000	0.41
Ornament contacts under control exposure	1.12	1,31	0.298	0.04
Superorbital plume contacts	1.63	1,31	0.212	0.05
Beak contacts	0.35	1,31	0.559	0.01
Total contacts	0.81	1,31	0.375	0.03
Relationship with natural SOP length				
Head bumps	3.50	1,30	0.071	0.10
Crest contacts	0.05	1,31	0.824	0.00
Ornament contacts	1.31	1,31	0.261	0.04

Beak contacts	0.05	1,31	0.831	0.00
Total contacts	0.18	1,31	0.677	0.01
Relationship with body size[a,b]				
Crest length	27.41	1,309	<0.0001	0.08
Superorbital plume length	27.95	1,300	<0.0001	0.08

Two-way ANOVA-randomized blocks, one-way ANOVA (with Bonferroni correction) and general leaner modal (regression) were used for the analysis (see text).

[a] PC1 of tarsus length, bill length and body mass.

[b] These birds were not exposed to the maze, were captured at the same location in multiple years (see text).

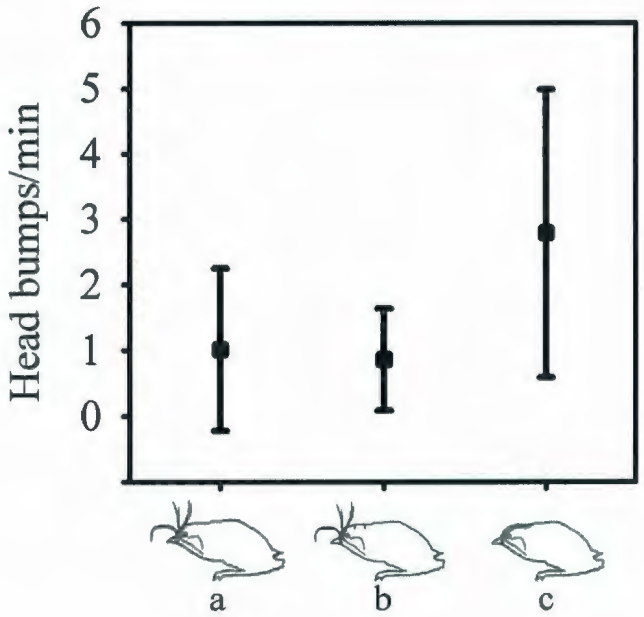

Figure 2.3

The success of Whiskered Auklets negotiating the maze (n=99) with (a) unmodified ornaments (control), (b) sham manipulation, and (c) taped down feather ornaments. The filled centre squares indicate the mean frequency of head bumps (± SD).

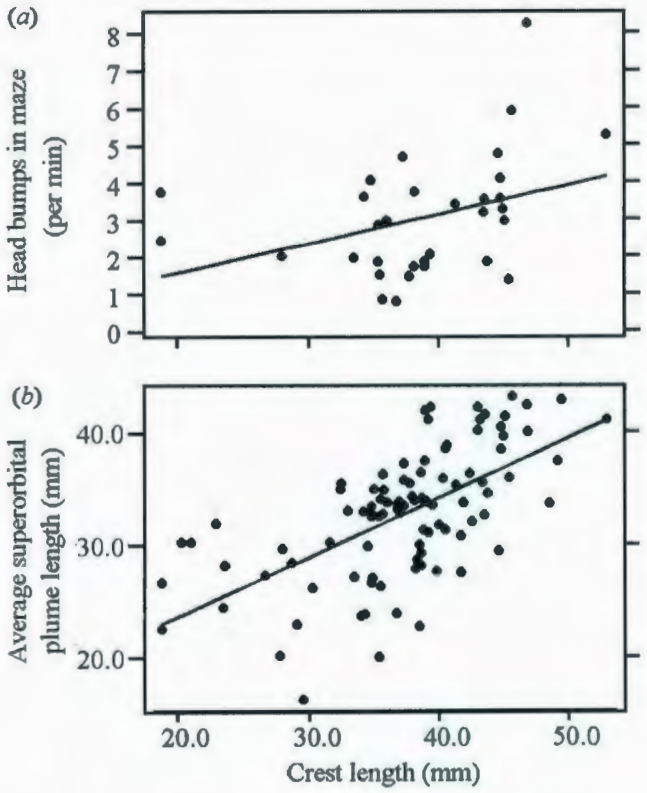

Figure 2.4

(a) Relationship of individual Whiskered Auklets' natural forehead crest length and frequency of head bumps within the darkened maze when the crest was taped down (n = 33), and (b) the regression between crest length and mean superorbital plume length (n = 98).

However, there were no significant relationships between frequency of feather ornament (crest and superorbital plumes) contacts, superorbital plume contacts considered separately, beak contacts or total contacts (head bumps, crest and superorbital plume contacts) with crest length (Tables 2.1-2.2). Similarly, head bumps, all feather ornament contacts, crest contacts considered alone, beak contacts and total contacts showed no significant relationship with superorbital plume length (Tables 2.1-2.2). More beak contacts were observed under ornament manipulation (two-way ANOVA; Tables 2.1-2.2) but it was difficult to distinguish beak contacts from deliberate pecking of maze walls. Among a large sample of birds captured and measured near the experimental study site, crest length (mean, 36.50 [±6.54 SD] mm) and superorbital plume lengths (mean average superorbital plume length, 31.43 [±6.32 SD] mm) were positively correlated with body size (Table 2.2).

2.5. DISCUSSION

Here I demonstrated that Whiskered Auklets' crest and superorbital plumes in combination helped individuals detect obstacles inside an experimental maze simulating their dark, complex, underground breeding crevices. With intact crest and facial plumes, Whiskered Auklets were able to navigate in the absence of visible light with few head bumps against the maze walls and roof. At their breeding colonies, adult Whiskered Auklets enter, navigate and nest in narrow rock crevices in cliffs, lava flows and talus at night: labyrinthine conditions with

sharp irregular obstacles and low or total absence of visible light. My results suggest that Whiskered Auklets use their ornamental facial feathering to aid underground navigation. Auklet breeding colony sites often include interlinked network of crevices used by multiple individuals of the same and other seabird species (Byrd and Williams 1993). Therefore, the sensory function of elaborate feathers might also aid in close-range detection of other birds within the confines of their crevices. I found that birds with well-expressed (longer) crest and facial plumes may have benefited more from these sensory structures, as those individuals showed greater dependence on them in the maze (Figure 2.4). This may be partly explained by the positive correlation between ornamental and body size (i.e., birds with long ornaments were simply larger in body size, so may have experienced a tighter squeeze in crevices). Nevertheless, it does raise the question of how variability in expression of the ornamental facial plumes might relate to their use for navigation. In contrast to adults, juvenile and subadult Whiskered Auklets have no or shorter protruding ornaments and enter crevices less frequently (Jones 1999; Zubakin and Konyukhov 1999; Pitocchelli et al. 2003).

Further work could address the question of the relative role of the forehead crest versus the white superorbital plumes. I was unable to investigate this here but because the crest is composed of contour feathers while the superorbital plumes are filoplumes, so a difference in sensitivity might be expected (Clark 2004). However, Brown and Fedde (1993) found a sensory role for secondary flight feathers that are contour feathers used for flight – indicating that contour

feathers can have a sensory use. The position of the Whiskered Auklets' forehead crest, makes it well placed to take on the role of detecting low overhead obstructions. Carefully designed studies to investigate extensive innervation or aggregation of mechanoreceptors on or near these feather tracts are urgently required to reveal the anatomical and physiological basis for the observed behavior. My results suggest a broader than recognized role for contour feathers in touch sensing and highlight a sensory use as a plausible explanation for other birds' 'ornamental' contour feather appendages. Other types of avian feather traits that deserve attention include swallow tail streamers (e.g., Rowe et al. 2001), quail crests (e.g., Hagelin and Ligon 2001; Paker et al. 2005) and other auklet species' feather ornaments (Gaston and Jones 1998; Jones 1999).

The Whiskered Auklet is the most nocturnally active crevice-dwelling species of auklet, and it possesses the longest crest and facial plumes (Jones 1999). Their breeding habitats (mostly, piles of small rock and boulder beaches) are unstable due to wave action, soil and wind erosion, and frequent earthquakes; therefore, the internal dimensions of breeding crevices can change unpredictably. Furthermore, Whiskered Auklets are the only *Aethia* auklet that regularly roost on land at night during the non-breeding season; and coincidentally it is the only auklet whose facial ornaments (especially the crest) are expressed during winter, consistent with a year-round sensory function. The Crested Auklet is the mostly diurnally active auklet species. It also frequents and breeds in deep dark rock crevices, and is the only other auklet species possessing a forehead crest (Jones

and Hunter 1993, 1999). The other diurnal auklets (Least [*A. pusilla*] and Parakeet [*A. psittacula*]), nest in shallow well-lit crevices, have no forehead crest and have short facial plumes (Gaston and Jones 1998; Jones and Hunter 1998; Jones 1999). The remaining species, Cassin's Auklet (*Ptychoramphus aleuticus*; no facial plumes) is nocturnal but breeds in relatively stable habitats, and uses self-excavated earthen burrows for breeding (Thoresen 1964), that have predictable internal dimensions and are more likely to have smooth internal surfaces of soft earth. Hence, I believe Cassin's Auklets face much less of a challenge to their underground movements and activities compared to the crevice-dwellers. These differences support the notion that mechanosensory function partly accounts for the long facial feathers of the Whiskered Auklet.

Feather ornaments of both Least and Crested Auklets (homologous to those of Whiskered Auklets) are favored by mutual mating preferences (Jones and Montgomerie 1992; Jones and Hunter 1993, 1999; Jones 1999). Experimental evidence is lacking, but Whiskered Auklet ornamentation may be favored by similar mating preferences, since this species displays similar ornaments during courtship and social activity (Jones 1999; Hunter and Jones 1999; Zubakin and Konyukhov 1999). Furthermore, these ornaments show the same high variability as ornaments in other auklet species (Jones and Montgomerie 1992; Byrd and Williams 1993; Jones et al. 2000), and as occurs for sexually selected traits in general (Alatalo et al. 1988). Taken together, these observations point to multiple factors (both sexual and natural selection) having roles in the origin or elongation

of auklet facial ornamentation. However, once protruding feathers evolved, sexual selection could explain the elaboration of traits in species with intense face-to-face courtship displays (Jones and Montgomerie 1992; Jones and Hunter 1993,1999; Andersson 1994).

To my knowledge, I have presented the first empirical evidence for a possibly widespread but overlooked sensory function of elaborate feather ornaments in birds. Similar traits, such as streamers on pin- and forked tails, elongated facial plumes and projecting feathers on the wings and body, that are routinely inferred to function primarily as visual signals during courtship (Darwin 1871; Kirkpatrick and Ryan 1991; Andersson 1994; Amundsen 2000), are all possible candidates for past and present sensory function. Indeed, future comparative and phylogenetic analyses of such trait expressions will likely reveal the role of sensory function as either a precursor for feather ornaments or a selective force that maintains such embellished traits in birds.

2.6. ACKNOWLEDGEMENTS

I thank G. W. Humphries for assistance in the field, G. V. Byrd and J. C. Williams for logistic support and permission to conduct research in the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge (AMNWR), K. Lewis and D. Schneider for advice in the analyses, Y. Artukhin for the Whiskered Auklet photograph, the captain and crew of the vessel M/V Tiglax for vessel transportation to Buldir Island, and M. Hauber and two anonymous reviewers for

constructive criticism. Major funding was provided by a Natural Sciences and Engineering Research Council (NSERC) Canada Discovery grant held by I. L. Jones.

CHAPTER THREE

VOCAL REPERTOIRES OF AUKLETS (ALCIDAE: AETHIINI): STRUCTURAL ORGANIZATION AND CATEGORIZATION

3.1. ABSTRACT

I categorized and quantified the complete vocal repertoires of breeding adult auklets (Aethiini, five species), to provide a baseline for a comparative study of the structure and function of vocalizations within this monophyletic group of pursuit-diving seabirds. Auklet vocal repertoires were complex and large (~25 call types across species) with 3-5 display types for each species. Displays were characterized by 1-5 frequency modulated, harmonically rich, element types arranged sequentially in varied combinations. Frequency attributes varied more than temporal attributes, within and across species. Calls of the nocturnal Whiskered Auklet (*Aethia pygmaea*) were most complex, but repertoires and complexity of nocturnal and diurnal species did not differ consistently. I recognized two major forms of vocal display: alternating arrangement of note types (e.g., Cassin's Auklet [*Ptychoramphus aleuticus*] and Parakeet Auklet [*A. psittacula*]); and sequentially graded arrangement of note types (e.g., Least Auklet [*A. pusilla*] and Whiskered Auklet). One species' repertoire (Crested Auklet [*A. cristatella*]) was composed of a mix of the two forms of display. There were vocal homologies in frequency modulation of notes, and arrangement and composition of notes in displays. My analysis revealed striking vocal similarities between: (a) two species not normally grouped together (Cassin's and Parakeet Auklets); and (b) Whiskered and Crested Auklets, which have been suggested to be closely related.

3.2. INTRODUCTION

Animal displays have long been analyzed as a source of characters that could elucidate interspecific relationships (Omland and Lanyon 2000, Price and Lanyon 2002, Päckert et al. 2003, Shelley and Blumstein 2005). However, vocal and other display traits are used relatively rarely for such inferences although vocalizations, in particular, typically are correlates of speciation and population divergence (Lanyon 1969, Payne 1986, Martens 1996, Isler et al. 2005, Isler et al. 2007), and are used routinely in modern species-level systematics such as species descriptions (Cuervo et al. 2005, Athreya 2006, Gonzaga et al. 2007). Vocalizations that are not learned are likely to be especially informative in elucidating relationships, and such vocalizations are widespread, as they typify all non-passerine birds with the exception of Psittaciformes and Apodiformes (Baptista and Schuchmann 1990, Farabaugh and Dooling 1996, Price and Lanyon 2002, Jarvis 2006). However, physical environment can influence the properties of acoustic signals, therefore, vocalizations of distantly related species that live in similar habitats tend to be more similar than those of closely related species that inhabit different habitats (Wiley and Richards 1982, Endler 1993a, b, Badyaev and Leaf 1997). Properties of acoustic signals vary with the context of signaling, thus vocal homoplasies could occur due to similar functions in different acoustic environments (Marler 1955).

Two comparative approaches have mainly been used to investigate vocal relationships between species: vocal homologues (Davis 1962, 1965, Winkler and

Short 1978, Slabbekoorn et al. 1999, Seddon 2005, Shelley and Blumstein 2005); or entire vocal repertoires (Price and Lanyon 2002). The latter is used less frequently, however, analysis of at least a few sound classes is necessary for the better understanding of acoustic differentiation across species in groups with large repertoires (Price and Lanyon 2002, Isler et al. 2007).

I conducted a comprehensive description of auklet vocalization to elucidate vocal relationships among auklets, which is the first such attempt for any group within the Alcidae. I assumed that inter-specific differences could be a result of natural and sexual selection on the structure of vocalizations in relation to vocal function (Badyaev and Leaf 1997, McCracken and Sheldon 1997), or alternatively could result as a non-selected consequence of phylogenetic divergence (Slabbekoorn et al. 1999, Price and Lanyon 2002, Seddon 2005). The objectives were to: (1) quantify and characterize the structural organization of vocal repertoires of auklets, (2) compare inter-specific variation among auklet vocal repertoires with respect to their phylogeny and ecology, and (3) identify vocal displays of significance to conservation-restoration projects. Phylogenetic significance of these repertoires and the evolution of vocalization of auklets have been described in Chapter Five. Here I provide a descriptive analysis of vocal behavior of auklets and attempt to describe the diversity of their non-learned vocalizations, standardize terminology, and emphasize some of the potential applications of this knowledge for management purposes.

3.3. METHODS

3.3.1. Study sites and recording methods

Recordings were made in the Aleutian Islands, Alaska: Buldir Island (52° 22'N, 175° 54'E), 25 May to 7 June in 2005, and 25 May to 24 July in 2006; and Egg Island (53°52'N, 166°03'W), 15 June to 11 July 2005. Both islands are grass-covered, treeless volcanic islands with beach boulders and exposed talus slopes, with large breeding colonies of auklets (Byrd and Day 1986, Bradstreet and Herter 1991). All five auklet species breed on Buldir Island; Cassin's, Parakeet and Whiskered Auklets breed on Egg Island. Recordings were made opportunistically during times of peak activity: Cassin's Auklet, 02:00-05:00 (Aleutian standard time); Crested and Least Auklets, 09:00-14:00; Parakeet Auklet, 06:00-12:00; and Whiskered Auklet, 00:00-02:00 and 04:00-06:00. I recorded birds that were separated by at least 10 m, to minimize the possibility of recording individuals more than once. Cassin's and Whiskered Auklets were recorded at night with the aid of a red lithium electrode diode headlamp (Zubakin and Konyukhov 1999). All recordings were made from undisturbed birds.

3.3.2. Equipment

I recorded birds with a Sony TCD-D10PROII Digital Audio Tape recorder (sampling rates 32, 44.1, or 44.2 kHz), or Fostex FR-2 solid-state recorder (sampling rate 48.1 kHz), with Senheiser MKH 70 or MKH 816 directional microphones (with wind guard and wind sock) and 3-30 m cables. Microphones

were tripod-mounted or hand-held. Recording sessions with individual birds were 30 min to 3 hr in duration, and contained multiple continuous recordings of 2-10 min in duration, each accompanied by behavioral observations. I recorded birds at distances of ~2-6 m. Recording sessions totaled ~80 hrs, from which I obtained recordings of vocal display of all species of auklets.

All birds were assumed to be breeding adults, as calling birds are mostly adults, and adults predominate on colony sites in the early and mid breeding season (Jones 1993a, 1993b, Manuwal and Thoresen 1993, Jones et al. 2001, Zubakin and Konyukhov 2001). Sex of calling birds was known only for Crested Auklets, based on the distinctive bill shape and courtship display (Jones 1993c).

3.3.3. Acoustic description and measurements

I selected recordings of good quality for analysis with Raven 1.2.1 (Bioacoustics Program, Cornell Lab of Ornithology, Ithaca, NY, USA). Settings for analysis for each species were as follows (Blackman window was used for all analyses): Cassin's and Parakeet Auklets - window size, 800 samples; 3 dB filter bandwidth, 90.5 Hz; time grid overlaps, 75%; frequency grid spacing, 43.1 Hz; Crested and Whiskered Auklets - 512 samples, 141 Hz, 90%, and, 86.1 Hz; and Least Auklet - 250 samples, 289 Hz, 50%, and, 172 Hz, respectively. The dominant harmonic was judged from the spectrogram slice view.

I used a combination of audible differences, overall visual impression of vocal sequences and constituent sound notes on spectrograms (Marler and Pickert

1984, Jones et al. 1989a, Hailman and Ficken 1996, Marler and Slabbekoorn 2004, Seddon 2005), and explicit measurements of physical properties to characterize the vocal repertoire. I referred to different basic sound elements as "notes" following Marler and Pickert (1984), and Marler and Slabbekoorn (2004). Measurements were duration, frequency, modulation of the carrier frequency, and harmonic structure (F_n, frequency of n^{th} harmonic; F_0, fundamental frequency; F_μ, frequency of the most strongly expressed harmonic, i.e. the harmonic with the highest intensity in the power spectrum; CF_n, carrier frequency of the n^{th} harmonic; FM, frequency modulation of CF). Frequency was estimated from spectrograms by selecting the beginning, end, highest, and lowest points of the signal. The frequency of the signal is the frequency of the selected rectangle's center (in Raven). I estimated FM by selecting the lowest and highest frequencies of the signal, and taking the frequency difference between these two points from the selection table (in Raven). Display types were identified for each species based on the composition of note types and audile plus visual characteristics, most of which were easily and reliably distinguishable in the field. My nomenclature follows previous published descriptions (Thoresen 1964, Byrd and Williams 1993, Jones 1993a, b, Jones et al. 2001, Manuwal and Thoresen 1993) but I provide new names for previously unrecognized types.

3.4. RESULTS

Auklet repertoires were complex and large (22 display types), and were characterized by 1-5 frequency modulated and harmonically rich note types (28 types across species) arranged sequentially in varied combinations (Figure 3.1). Most sound notes were strongly harmonic, brief, and with pronounced FM (Table 3.1 and Figure 3.1). Characteristics of notes and appearance of them in displays were intraspecifically consistent.

3.4.1. Cassin's Auklet

Vocalizations of Cassin's Auklets consisted of five note types (CaauNote-a to –e), which formed the basis of three vocal displays (CaD-a to –c), all being harsh screeching sounds. The most notable aspect of Cassin's Auklet vocalizations was the distinctive production of long displays composed of repeated alternate use of two contrasting note types. These sounded like wheezy sequential inhalations and exhalations (although it could not be confirmed if the vocalizations were in fact associated with such a breathing pattern) with abrupt variation in harmonic structure and FM between these repetitive note types, which were delivered together to form a discontinuous arch in the spectrogram (Figure 3.2C). F_0 was the most strongly expressed harmonic (F_μ) however, in some notes, part of the syllable had F_0 and the other half had F_3 as F_μ (Figure 3.2C). The vocal display was characterized by organized introduction, middle, and terminal end, and alternate repetitive arrangement of note types (Table 3.2).

Table 3.1

Mean ± SD (range) for descriptions of note types of auklets (Aethinii). F_μ, most expressed frequency; FM, frequency modulation of F_μ ; F_0, fundamental frequency; F_n, frequency of n^{th} harmonic.

Auklet species	Note code	Duration (ms)	F_μ (kHz)	FM (kHz)	F_μ	Harmonic structure	*n*
Cassin's	CaauNote -a	225 ± 52 (135-305)	2.2 ± 0.17 (1.9-2.4)	1.0 ± 0.39 (0.6-2.0)	F_0	Weak	10
	-b	560 ± 263 (285-1075)	2.3 ± 0.25 (1.9-2.7)	1.1 ± 0.58 (0.5-2.0)	F_0	Strong	10
	-c	655 ± 145 (495-1015)	2.5 ± 0.21 (2.1-2.8)	1.1 ± 0.31 (0.6-1.4)	F_0	Strong	11
	-d	170 ± 25 (135-230)	2.3 ± 0.19 (2.0-2.6)	1.4 ± 0.42 (0.8-2.1)	F_0	Strong	11
	-e	35 ± 8 (20-45)	3.1 ± 0.39 (1.6-3.5)	0.5 ± 0.09 (0.4-0.6)	F_0-F_3	Strong	7
Crested	CrauNote -a	170 ± 40 (110-255)	1.4 ± 0.49 (0.6-2.1)	0.7 ± 0.18 (0.3-0.9)	F_0-F_2	Weak	10
	-b	90 ± 50 (45-220)	1.6 ± 0.29 (1.1-2.1)	0.6 ± 0.18 (0.4 -0.9)	F_0-F_2	Strong	11
	-c	730 ± 190 (510-1030)	1.1 ± 0.12 (0.9-1.3)	0.6 ± 0.01 (0.4 – 0.7)	F_0-F_2	Weak	10
	-d	340 ± 120 (180-755)	1.5 ± 0.23 (1.2-2.3)	1.1 ± 0.17 (0.2-1.2)	F_0-F_2	Weak	20
	-e	360 ± 128 (170-505)	1.6 ± 0.59 (0.6-2.0)	0.5 ± 0.13 (0.2-0.7)	F_0-F_2	Weak	10

Auklet species	Note code	Duration (ms)	F_μ (kHz)	FM (kHz)	F_μ	Harmonic structure	*n*
Least	LeauNote -a	15 ± 4 (10-25)	3.5 ± 0.79 (3.1-5.7)	1.1 ± 0.30 (0.7-1.6)	F_0-F_1	Strong	10
	-b	40 ± 11 (25-55)	3.8 ± 0.11 (2.8-5.6)	1.1 ± 0.26 (0.6-1.5)	F_0-F_2	Strong	9
	-c	70 ± 18 (45-105)	4.0 ± 0.95 (3.0-5.3)	1.8 ± 1.39 (0.7-5.5)	F_0-F_3	Strong	10
	-d	125 ± 17 (90-150)	4.3 ± 0.89 (3.3-5.3)	2.3 ± 0.61 (1.4-3.0)	F_0-F_4	Strong	10
	-e	370 ± 77 (265-515)	3.5 ± 0.33 (3.2-4.0)	1.4 ± 0.45 (1.0-2.5)	F_0	Weak	10
Parakeet	PaauNote -a	45 ± 25 (20-115)	2.1 ± 0.56 (1.6-3.3)	1.2 ± 0.36 (0.7-2.0)	F_0	Weak	12
	-b	60 ± 28 (25-120)	5.7 ± 0.18 (0.4-1.0)	0.4 ± 0.10 (0.3-0.6)	F_0	Strong	10
	-c	1250 ± 465 (750-1950)	2.9 ± 0.30 (2.3-3.5)	2.2 ± 0.41 (1.8-2.9)	F_0	Strong	10
	-d	375 ± 103 (255-610)	0.5 ± 0.04 (0.5-0.6)	0.5 ± 0.06 (0.4-0.6)	F_0	Strong	10
Whiskered	WhauNote -a	45 ± 17 (25-80)	3.4 ± 0.25 (2.8-3.9)	0.9 ± 0.30 (0.4 -1.5)	F_3	Strong	20
	-b	230 ± 82 (140-380)	3.8 ± 0.27 (3.5-4.3)	1.1 ± 0.26 (0.8-1.5)	F_3	Strong	10
	-c	150 ± 35 (100-200)	4.0 ± 0.44 (3.2-4.7)	1.6 ± 0.34 (1.2-2.1)	F_3	Strong	10
	-d	315 ± 94 (190-510)	4.0 ± 0.30 (3.6-4.4)	1.5 ± 0.28 (1.1-2.0)	F_3	Strong	10

Auklet species	Note code	Duration (ms)	F_μ (kHz)	FM (kHz)	F_μ	Harmonic structure	*n*
	-e	190 ± 62 (40-280)	3.7 ± 0.43 (2.7-4.3)	1.1 ± 0.18 (0.7-1.3)	F_3	Strong	10
	-f	540 ± 99 (460-675)	3.5 ± 0.36 (2.9-3.8)	0.7 ± 0.23 (0.6-1.0)	F_3	Weak	5
	-g	545 ± 114 (370-690)	4.0 ± 0.27 (3.6-4.2)	1.7 ± 0.18 (1.4-1.9)	F_3	Strong	5
	-h	435 ± 112 (270-515)	3.1 ± 0.13 (2.9-3.2)	0.7 ± 0.26 (0.3-1.0)	F_3	Strong	4
	-i	300 ± 29 (270-320)	3.8 ± 0.60 (3.5-4.5)	1.8 ± 0.29 (1.6-2.1)	F_3	Weak	3

Table 3.2

Mean ± SD (range) for duration and mean ± SD (range) for element composition of auklet (Aethiini) vocalizations. WhauNote type-f and -i are not included due to small sample sizes.

Auklet species	Display type	Duration (s)	Note Types (*n*)	Note spacing (ms)	Note type composition							*n*
					-a	-b	-c	-d	-e	-g	-h	
Cassin's	Krreerr-er	4.3 ± 1.5 (2.5-6.3)	2	27-574				0.3 (0-2)	15.7 (0-41)			6
	Kut-I-er	18.5 ± 12.2 (7.5-49.2)	4	49-891	5.7(1-12)	6.6(3-13)	2.9 (0-6)	11.6 (6-26)				10
	Kut-reearh	13.8 ± 8.8 (8.0-29.4)	4	108-464	3.2(0-9)	0.8(0-4)	7.0 (4-10)	8.2 (6-13)				5
Crested	Trumpet	3.15 ± 0.7 (1.7-3.9)	4	2.2-28.7	4.0(2-7)	1.9 (0-9)	1.0 (1)	3.7 (1-5)				10
	Cackle	6.7 ± 1.8 (4.1-9.6)	3	3.5-28.5	4.8(0-12)	33.3 (12-50)			1.8 (0-6)			10
	Hoot	8.1 ± 2.0 (4.5-10.4)	3	2.8-30.5	4.2(0-14)	23.9 (11-50)			5.4 (1-11)			9
	Bark	0.4 ± 0.1 (0.2-0.5)	1	11.3-135.1				14.0 (5-30)				10
	Whine	8.5 ± 5.34 (4.0-21.5)	3	9.1-69.1	3.3(0-31)	16.8 (0-42)			2.7 (0-27)			10
Least	Chatter	3.1 ± 1.3 (1.7-6.4)	4	2.2-16.1	4.0(0-15)	1.6 (0-5)	5.2 (0-24)	10.4 (7-27)				10

Auklet species	Display type	Duration (s)	Note Types	Note spacing	-a	-b	-c	-d	-e	-g	-h	*n*
						0.5 (0-1)	0.5 (0-1)	0.5 (0-1)	9.5 (8-11)			3
	Chirp	1.1 ± 0.4 (0.6-2.2)	4	5.4-26.3	15.3(0-50)	7.6 (0-18)	3.0 (0-16)	0.4 (0-3)				7
	Chirr-buzz	0.4 ± 0.1 (0.3-0.5)	1						1			12
Parakeet	Chip	11.7 ± 8.7 (1.3-23.2)	3	41-1611	40.7 (11-97)	0.9 (0-1)		0.5 (0-3)				10
	Whinny	8.7 ± 2.1 (4.7-11.9)	4	15-294	23.7 (2-45)	7.5 (0-16)	4.2 (2-8)	5.1 (3-10)				10
	Short Whinny	4.1 ± 2.4 (1.3-9.5)	4	28-720	20.9 (1-47)	3.6 (0-13)	1.3 (0-3)	1.1 (0-3)				10
	Raft Whinny	6.5 ± 3.0 (3.2-10.5)	3	200-1010	24.7 (0-70)		2.8 (0-8)	0.3 (0-2				10
Whiskered	Staccato Beedoo	3.9 ± 1.5 (2.2-6.9)	5	69-110	10.2 (3-29)	1.2 (0-3)	5.8 (3-10)	2.8 (1-5)	1.0 (0-4)			9
	Metallic Beedoo	6.2 ± 3.5 (2.7-13.2)	6	55-880	14.9 (4-27)		1.1 (0-5)	2.0 (0-4)	10.4 (0-32)	0.2 (0-1)	0.13 (0-1)	8
	Duet Beedoo	3.0 ± 2.1 (1.1-7.3)	6	40-510	11.2 (3-29)	2.4 (0-14)	2.8 (0-5)	0.3 (0-3)	1.5 (0-9)	0.4 (0-2)	-	10
	Bark	0.8 ± 0.1 (0.7-0.9)	2	76-87	1.0 (1)	3.0 (3)						3
	Mew	Variable	8	Variable								45

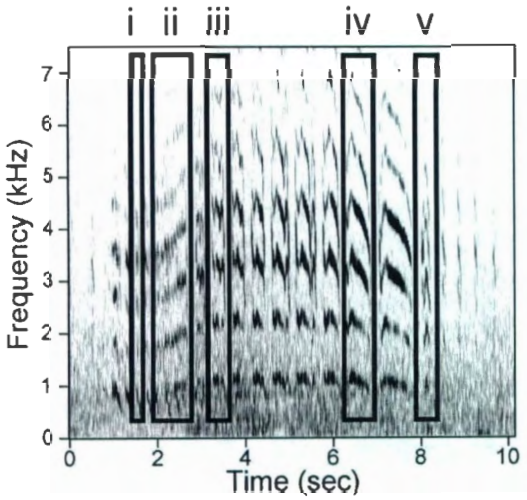

Figure 3.1

Example of the arrangement of note types in auklet vocal display; Staccato Beedoo display of Whiskered Auklet. Boxed sections i-v represent sound note-a to –e, respectively.

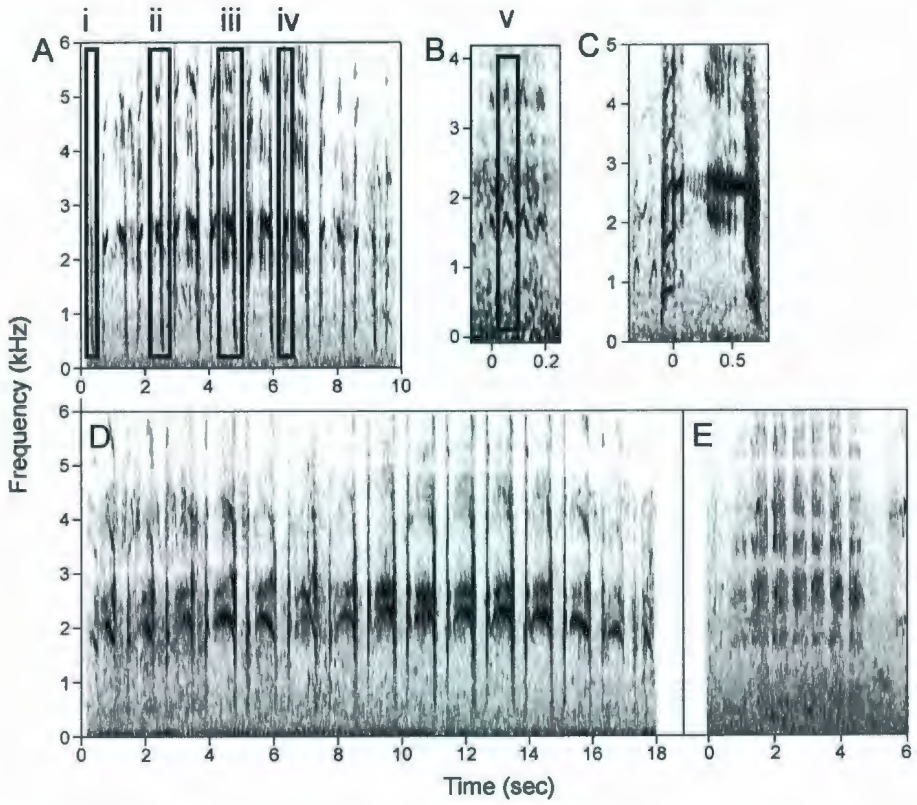

Figure 3.2

Vocal repertoire of Cassin's Auklet. (A) Kut-I-eer, (B) section of the Krreerr-er display in a different time and frequency scale to illustrate note type-e, (C) section of the Kut-I-eer display (note type-c and –d) in a different time and frequency scale to illustrate frequency modulation and changing F_{μ}, (D) Kut-reeah, and (E) Kreerr-er, boxed sections i-v represent note type-a to –e, respectively.

Display type a (CaD-a; Figure 3.2A; **Kut-i-eer**). Note-a to –d were predominant in this long (8-49 s) display. Note-a, -b and -d initiated the display, followed by the main body of alternately arranged Note-d and -b, or -d and -c; the end was brief, consisting of note-a and –b (Figure 3.2A). Frequency remained fairly constant throughout the display; frequency distribution and the composition of note types were: note-a, 1.7-2.4 kHz, with 0-12 notes; note-b, 1.8-2.6 kHz, with 3-11 notes; note-c, 2.2-2.7 kHz, with 0-6 notes; and note-d, 1.5-2.5 kHz, with 6-21 notes (Table 3.2). The introduction and end consisted of brief pulses of note -a and -d, forming a "*kut..kut..kut..*" segment (not distinct in Figure 3.2A). Kut-i-eer display was the commonest display in the Cassin's Auklet vocal repertoire, delivered as single utterances or as duets from within the breeding burrow at night (Table 3.3). Several birds at close quarters delivering this display together form a "Kreek Chorus".

Display type b (CaD-b; Figure 3.2D; **Kut-reeah**). Note type-c was predominant in this display. Note-a and –d consisted of introduction and end, however, the structure of the display was less defined than CaD-a. The display duration was 8-29 s. Frequency and the organization of note types were: note-a, ~2.3 kHz, 0-9 notes; note-b, ~2.2 kHz, 0-4 notes; note-c, 2.3-2.7 kHz, 4-10 notes; and note-d, 2.1-2.7 kHz, 6-13 notes (Table 3.2). The long duration of the predominant note-c makes the shrill nature of the Kut-reeah had a deep '*reeah*' quality compared to the metallic *'eer'* of the kut-i-eer.

Table 3.3

Occurrence of auklet vocal display in special, temporal, and behavioral situations. Qualitative score for the occurrence of the display in the given context: *** predominant; ** common; *rare, (*) occurrence is likely.

Auklet species	Display	Occurrence								
		Time		At the colony		At sea	In flight	Social interactions		
		Day	Night	Surface	In crevice			Courting	Advertisement	Contact/alarm
Cassin's	Kut-I-er		***	*	***			***	**	(**)
	Kut-reearh		***		***				***	
	Krreerr-er		***				***			***
Parakeet	Whinny	***	*	***	*			***	***	
	Raft Whinny	***	*			***		(**)	***	
	Short Whinny	***		**	***	**		(**)	(**)	
	Chip	***		**	***					**
	Squeal	**				**	***			***
Crested	Cackle	***	*	***	**	*		***		

Auklet species	Display	Time		At the colony		At sea	In flight	Social interactions		
		Day	Night	Surface	In crevice			Night	Surface	In crevice
	Trumpet	***	*	***	**	*		**	***	
	Hoot	***	*	*	***				***	
	Whine	**	**		***					***
	Bark	**		***	***	***	***			***
Whiskered	Duet Beedoo		***	*	***	**		***		(*)
	Metallic Beedoo		***	***	***	**		(**)	***	
	Staccato Beedoo		***	***	***	***		(*)	***	
	Mew	**	***	***	***	*				***
	Bark		*				**			**
Least	Chatter	**		***				**	***	
	Deep Chatter	**		***				*	***	
	Chirp	***	*	**		***	***			***
	Chirr-buzz	**	*	***	**					***

Display type c (CaD-c; Figure 3.2E; **Kreerr-er**) was brief (2-6 s) and consisted mostly of note-e, arranged in groups of 6-10 notes (Figure 3.2B), with F_{μ} of 2.1-2.5 kHz. It sounded like a rapid "*kreer..er...kreer..er...*" sound. CaD-c was sometimes performed as a duet, and single notes were used as a flight call at night (Table 3.3) mostly by birds departing the colony.

3.4.2. Parakeet Auklet

I recognized four note types (PaauNote-a to –d; Table 3.1; Figure 3.3), forming five display types (PaD-a to –d; Table 3.2). Similar to the above species, this repertoire was characterized by the production of long display consisted of repetitive and alternately arranged sounds with abrupt FM and harmonic structure. These sounded like wheezy sequential inhalations and exhalations.

Display type a (PaD-a; Figure 3.3A; **Chip**) consisted of an arrangement of short pulses, and it was delivered from inside crevices and in front of entrances to burrows or crevices (Table 3.3). The duration was 1-28 s. It consisted of note-a, but note-b and -d occasionally occurred between sequences of note-a (Table 3.2, Figure 3.3A). Introductory, middle, and terminal parts were not clearly demarcated, and no systematic changes in CF occurred over the course of the display (Figure 3.3A). The display sounded like "*kut..kut..kut..*".

Display type b (PaD-b; Figure 3.3B; **Whinny**). This long display was the commonest Parakeet Auklet vocalization. The duration was 5-12 s. The Whinny

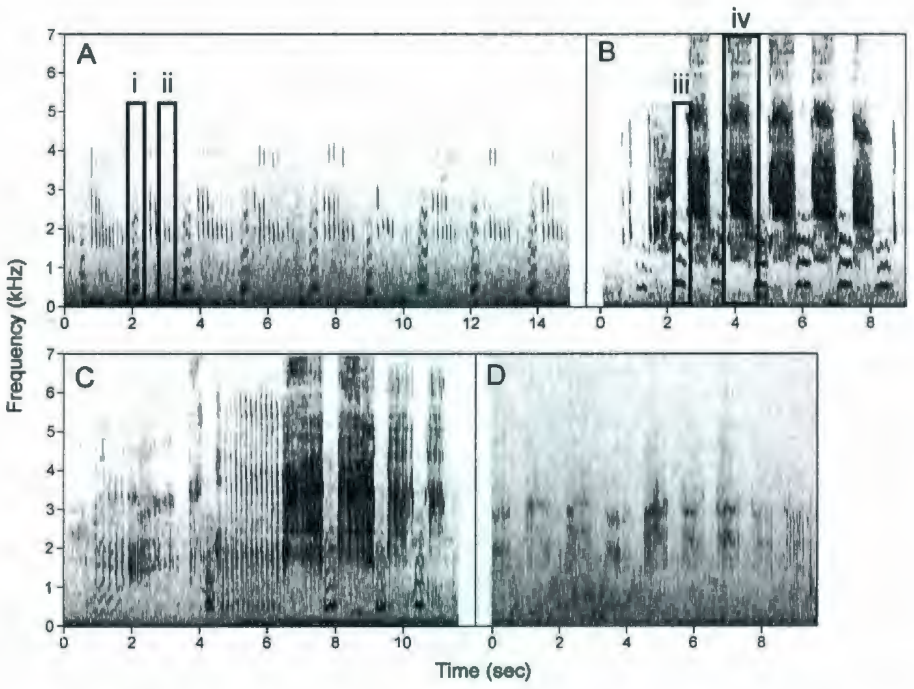

Figure 3.3

Vocal repertoire of Parakeet Auklet. (A) Chipping, (B) Whinny, (C) Short Whinny, (D) Raft display, boxed sections i-iv represent note type-a to –d, respectively.

consisted of note-a to –d, and note-c and –d, alternately arranged in the middle part of the display (Figure 3.3B). The introductory, middle, and terminal parts differed respectively by: note-a and rarely note-b; note-c and note-d; note-a (Figure 3.3B). Frequency and the organization of notes were: note-a, 1.7-3.0 kHz, 2-35 notes; note-b, 0.4-0.6 kHz, 0-16 notes; note-c, 1.9-3.5 kHz, 2-8 notes; and note-d, 0.5-0.8 kHz, 3-10 notes. Frequency increased to the middle of the display, and then decreased. This display was performed mainly as a duet (Table 3.3). It sounded like a nasal "*hiph..pheee..*".

Display type c (PaD-c; Figure 3.3C; **Short Whinny**) was characterized by its brevity (1-7 s) and variable arrangement of note types. Introduction, middle, and terminal parts usually were not well defined. The middle part consisted of note-c and –d; note-a was common in introductory and terminal parts (Figure 3.3C), and sometimes the display consisted entirely of note-b (Table 3.2). Frequency increased gradually over the display and decreased rapidly near the end (Figure 3.3C). The frequency and the organization of notes were: note-a, 1.7-3.2 kHz, 2-47 notes; note-b, 0.5-0.6 kHz, 0-8 notes; note-c, 1.8-3.1 kHz, 0-3 notes; and note-d, 0.4-0.6 kHz, 0-3 notes. Short Whinny was delivered singly or as a duet (Table 3.3).

Display type d (PD-d; **Raft Whinny**; Figure 3.3D). This display type was subsumed within the Whinny display by Jones et al. (2001: Duet-Whinnying and Whinnying). I distinguished it here because it consisted of only note-a and –c,

with poor structural organization (introduction, middle and terminal end), and was delivered only in rafts of 10-25 birds swimming close together (Figure 3.3D; Table 3.3). In contrast, note-c and -d predominated in the Whinny, which had characteristic organization of note types (Figure 3.3B). Duration was 3-10 s; introductory, middle, and terminal parts were not well differentiated. The frequency and the organization of notes were: note-a, 1.9-2.8 kHz, 2-70 notes; note-c, 2.7-3.4 kHz, 0-8 notes; and note-d, 0.6-0.6 kHz, 0-2 notes (Tables 3.1-3.2).

Display type e (PaD-e; **Squeal**) consisted of note-d, but the note was longer and had less FM. This call was given by disturbed birds taking flight, especially in the presence of predators (primarily Glaucous-winged Gull [*Larus glaucescens*] at Buldir Island, and Peregrine Falcon [*Falco peregrinus*] at Egg Island; Table 3.3). Birds also squealed when caught in mist nets, interspersed with aggressive bites towards human handlers. I did not obtain good quality recordings of squeals hence excluded them from the analyses.

3.4.3. Crested Auklet

Five note types (CrauNote-a to –e) were characterized (Table 3.1) that were incorporated into five display types (CrD-a to –e; Table 3.2). Distinctive FM and gradual increase followed by decrease in CF characterized these displays (Figure 3.4). The highest energy was in F_0, F_1, or F_2 (Table 3.2). However, in Trumpet (CrD-a), note-a and -d arranged alternately and delivered repetitively. Calls of

this species included a variety of barking, hooting and cackling sounds, and among auklets, only Crested Auklets had pure-tone vocalizations (Figure 3.4C).

Display type a (CrD-a; Figure 3.4B; **Trumpet**). This long (2-4 s), structurally well-defined display included four note types (Table 3.2). The Frequency and the organization of notes were: note-a, 0.9-1.2 kHz, 2-7 notes; note-b, 2.1-1.4 kHz, 0-9 notes; note-c, 1.1-1.4 kHz, 1 note; note-d, 0.6-2.5 kHz, 1-6 notes. The introductory, middle, and terminal parts were respectively: note-a and –c; note-a and –d; and note-b (Tables 3.1-3.2). In the middle, note-d predominated and was alternately expressed with note-a (Figure 3.4B). Trumpeting was one of the commonest displays, and was delivered mainly by males (Table 3.3) in a distinctive posture; it sounded like "ahee..hew...*KUHOO...kuru. .kuru..kru..kru*". The hollow "*kuhoo*" sound of the trumpet was associated with the nearly pure-tone section of the note-c (Figure 3.4C).

Display type b (CrD-b; Figure 3.4D; **Cackle**) was characterized by rapid rhythmic series of note-b of varying duration (4-10 s). The introduction, middle and terminal parts were consisted of note-b, but note-a and -e occurred infrequently in the middle (Figure 3.4D). The frequency and the organization of notes were: note-a, 0.9-1.1 kHz, 0-12 notes; note-b, 1.3-2.0 kHz, 22-60 notes; and note-e, 0.7-2.2 kHz with 0-6 notes (Table 3.2). Cackle calls with note-e were structurally closer to Hoot (Figure 3.4E), but the expression of note-e was weaker, and the spacing between note-b in Cackle was greater than in Hoot (Table 3.2).

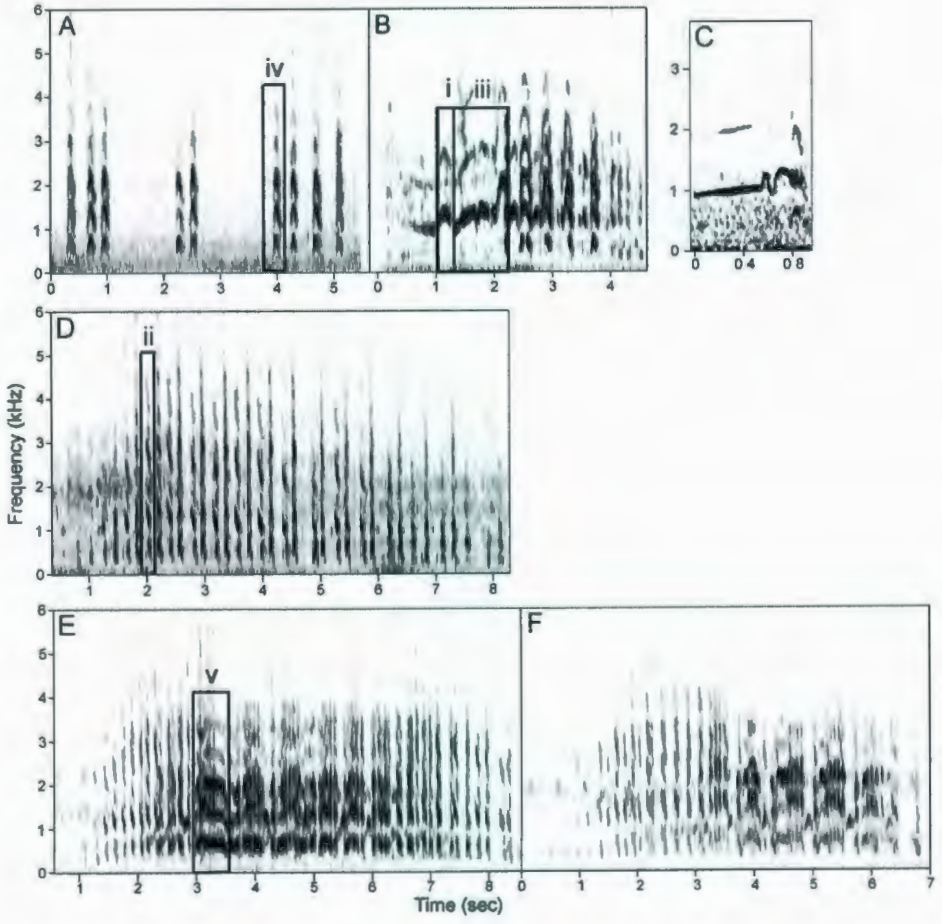

Figure 3.4

Vocal repertoire of Crested Auklet. (A) Bark, (B) Trumpet, (C) part of the Trumpet with a different time and frequency axis to show the nearly pure-tone section of note type-c (D) Cackle, (E) Hoot, and (F) Whine, boxed sections i-v represent note type-a to –e, respectively.

Cackle was delivered as a series of staccato metallic notes, frequently performed as a loud duet by pairs (Table 3.3); it sounded like "*kut-tee. kut-tee.. kre- kre-kree...*".

Display type c (CrD-c; Figure 3.4E; **Hoot**) was characterized by the prominent expression of nearly pure-tone note-e, which resulted in a hooting quality. The duration was 4-10 s. The introduction, middle, and terminal parts were distinct (Figure 3.4E). Frequency rose gradually through the display, remained fairly constant in the middle, and decreased at the end. F_{μ} varied from F_0-F_2 in different notes. The frequency and the organization of notes were: note-a, 0.7-1.8 kHz, 0-14 notes; note-b, 1.1-2.1 kHz, 11-50 notes; and note-e, 0.6-2.1 kHz, 1-11 notes (Table 3.2). Hooting was delivered mostly from crevices especially just after peak colony activity in midday (Table 3.3). It sounded like "*kuhoo... hooo... ooo..*".

Display type d (CrD-d; Figure 3.4F; **Whine**) was characterized by simple composition of sound notes, repetition of the same notes throughout the display, loose display structure (Figure 3.4F), and distinctive plaintive "*keew...keew...*" sound. The duration was 1-21s. Whine display comprised of note-a, -b and –e (Table 3.2); note-b was the dominant note type. The introduction, middle and the terminal end were poorly defined. The frequency and the organization of notes were: CS-a, 1.3-1.6 kHz, 0-12 notes; CS-b, 1.2-3.2 kHz, 12-50 notes; and CS-e, F 1.3kHz, 0-1 notes.

Display type e (CrD-e; Figure 3.4A; **Bark**) was the commonest and structurally simplest Crested Auklet display, delivered by both sexes in the colony and at sea (Table 3.3). CrD-e was structurally similar to Whiskered Auklet Bark (Figure 3.5D) but lower in frequency. The duration was ~0.5 s. It consisted solely of note-d; F_{μ} 0.6-2.0 kHz; no differentiated introduction, middle, or terminal parts (Figure 3.4A). CD-e sounded like the yap of a small dog.

3.4.4. Whiskered Auklet

Five vocal display types (WhD-a to –e) were identified, with nine note types (WhauNote-a to –i; Tables 3.1-3.2). The marked FM, sequential gradation of note complexity along the display, and gradual increase followed by decrease in CF, characterized these displays (Figures 3.1,3.5). The highest energy was in F_2 or F_3. Whiskered Auklet calls sound very high pitched compared to the vocalizations of other auklets.

Whiskered Auklet display type a (WhD-a; Figure 3.1; **Staccato Beedoo**) was a complex long display (duration 2-7 s), comprising several note types (Table 3.2). This and the next display type (WhD-b) have been described together as "Staccato beedoo" by previous authors (Byrd and Williams 1993). I distinguished it here because note-b was present in the introduction of WhD-a, giving the characteristic vibrating "*kirree*" sound to it, which was absent from the Metallic Beedoo (WhD-b; Figure 3.5A). The introductory, middle, and terminal parts of the display were distinguished respectively by: note-a and –b; note-c and –d;

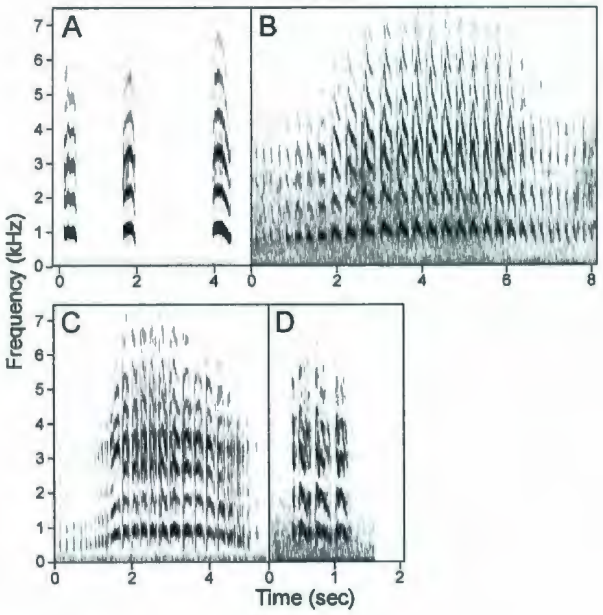

Figure 3.5

Vocal repertoire of Whiskered Auklet. (A) Example of a Mew call, (B) Metallic Beedoo, (C) Duet Beedoo, and (D) Bark.

note-e and –a (Figure 3.1). Frequency increased within and across note types until approximately the middle of the display, and then decreased thereafter (Figure 3.1), as follows: note-a, 2.8 kHz-3.8 kHz; note-b, 3.1 kHz- 3.9 kHz; note-c, 3.2-4.3 kHz; note-d and -e, 3.1- 4.2 kHz (Figure 3.1). This was the commonest vocal display, and was given throughout the night, most commonly during times of peak activity at the colony (Table 3.3).

Display type b (WhD-b; Figure 3.5B; **Metallic Beedoo**). In this display, the composition of note types and duration were variable, and introductory, middle and terminal parts were not clearly distinguishable. Note-e was common (Figure 3.5B), imparting the characteristic "*tuwee....*" sound. Note-a was the common note type in the introduction, but note-d, -e, -g, and -i also occurred. Note-e, -c, and –d occurred in the middle of the call, and note-f near the end (Tables 3.1-3.2). The major difference between this and the preceding display type (Staccato Beedoo, WhD-a) was the consistent lack of note-b; consequently, the Metallic Beedoo display lacked the vibrant "*Kiree...*" introductory sound. This display was uttered predominantly in the colonies before dawn (Table 3.3).

Display type c (WhD-c; Figure 3.5C; **Duet Beedoo**). This brief display (duration 1-6 s) consisted of three or four types of notes, and was dominated by note-b and –c (Table 3.2). The introductory, middle, and terminal parts were distinguished respectively by: note-a; note-b, -c, and –d; and note-a (Figure 3.5C). Frequency increased rapidly across notes from 2.7-3.3 kHz at the introduction up to 3.4-4.0 kHz until near the middle of the display, and then gradually decreased

to 2.8-3.5 kHz (Figure 3.5C). Note-b and –c imparted a rapid vibrant "*Kree..kree.kree..*" quality to the display. This display was characterized by its brevity and of the frequent presence of note-b. It was performed mostly as a duet from inside crevices (Table 3.3). This display became increasingly common over the breeding season.

Display type d (WhD-d; Figure 3.5D; **Bark**) was an uncommon brief display with two syllables (Table 3.2). The duration was 0.7-0.9 s. Note-a formed the introduction, the middle part consisted of note-c, and the terminal part was not clearly defined (Figure 3.5D). The frequency of the brief introductory note-a started at ~3.0-3.9 kHz, and then peaked at 3.6-3.7 kHz with note-c. This tremulous display was delivered just before taking off from crevices (Table 3.3); it sounded like the bark of a dog.

Display type e (WhD-e: Figure 3.5A; **Mew calls**). All note types were delivered individually as Mew calls except note-h (Tables 3.1-3.2). I treated these simple displays as eight variants (WhD-e-1 to 8), corresponding to note-a to –i, respectively. The duration and the composition of notes varied from a single Mew call (less than a 0.5 s), 2-3 mews at a time (2-3 s, Figure 3.5B), to repetition of the same Mew call for ~10 times (more than 10 s). Mew calls were given by single birds, birds duetting, and by multiple birds in chorus (Table 3.3). The sound quality varied from pulse-like single "*Kik..*", "*Mew*", and tremulous "*Kreew..*" to nasal "*Eew..*'.

3.4.5. Least Auklet

Four display types were distinguished (LeD-a to –d). These consisted of five intergrading note types (note-a to –e; Tables 3.1-3.2; Figures 3.6-3.7). F_{μ} varied from F_0-F_1. This species performed a variety of harsh, atonal, chattering and chirp-like vocalizations. The higher frequency of F_{μ}, sequential gradation of notes, and relative simplicity of the organization of notes characterized Least Auklet displays.

Display type a (LeD-a; Figure 3.6A; **Chatter**) was the commonest display type, with the duration of 2-6 s. It consisted of note-a to -d; introduction, middle, and terminal parts were differentiated in the distribution of notes and CF (Table 3.2; Figure 3.6A). Note type duration, complexity and CF increased until the middle of the display, and decreased thereafter. The frequency and the organization of notes were: note-a, 2.3-3.1 kHz, 0-15 notes; note-b, 2.7-3.2 kHz, 0-5 notes; note-c, 2.8-3.3 kHz, 0-24 notes; and note-d, 3.1-3.5 kHz, 7-27 notes (Table 3.2). Chatter display was delivered only by males (Table 3.3), and was a high pitch trill associated with a distinctive posture; it sounded like "*scht-tshhhht-tshhhh-tshhht-tshht...*".

Display type b (LeD-b; Figure 3.6B; **Deep Chatter**) was the structurally most complex vocalization of this species. The duration was 2-4 s. It comprised note-b, -c, -d, and –e (Table 3.2). The introductory, middle and terminal parts of the display were distinguished respectively by note-b; -d, and –e; and –c (Figure 3.6B). The frequency and the organization of notes were: note-b, 2.8-2.9kHz, 1-2

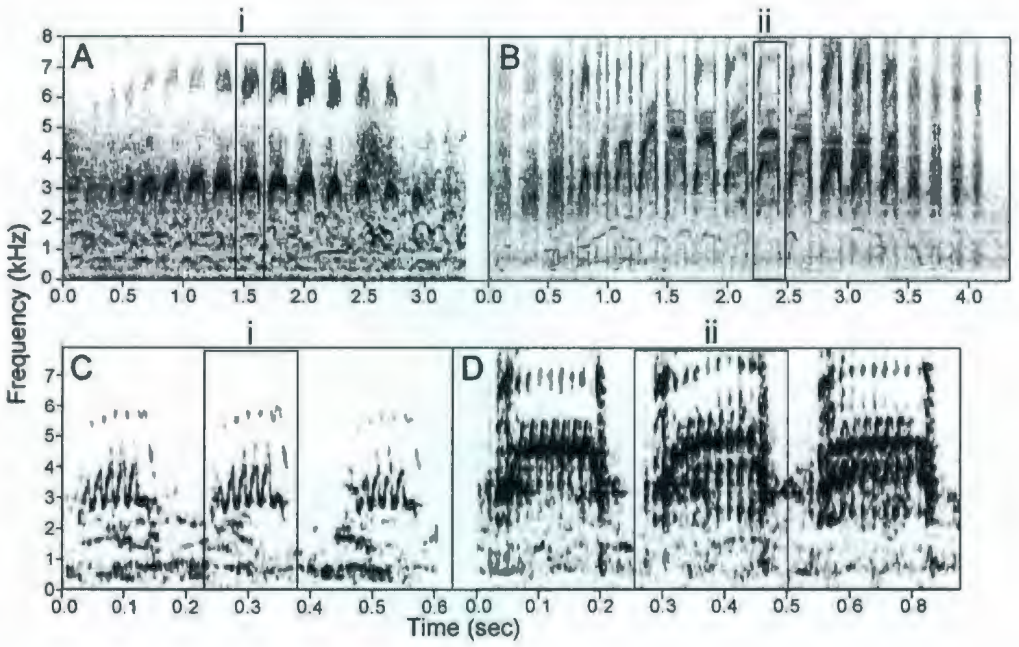

Figure 3.6

Vocal repertoire of Least Auklet. (A) Chatter, (B) Deep Chatter, (C) section of the Chatter display in different time and frequency scale, and (D) section of the Deep Chatter in different time and frequency scale, boxed sections i and ii represent note type-c and –d.

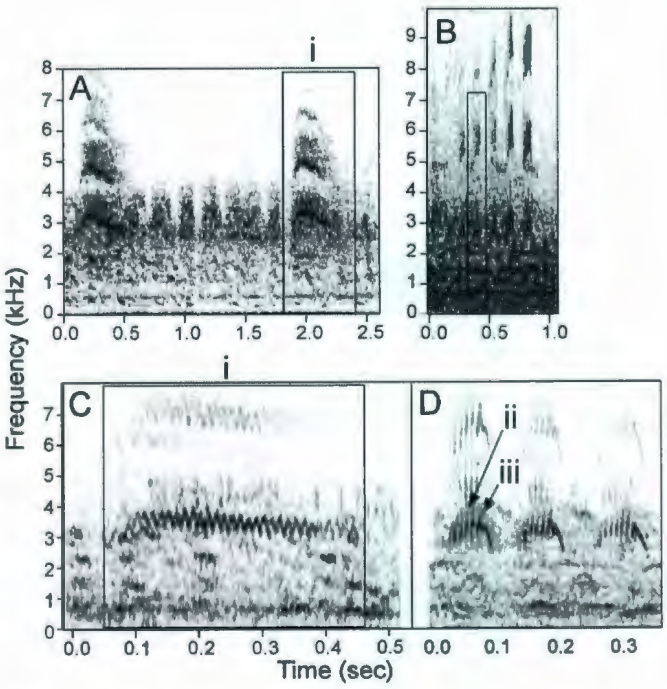

Figure 3.7

Vocal repertoire of Least Auklet. (A) Chirr-buzz, (B) Chirp, (C) section of the Chirr-buzz display in different time and frequency scale, (D) section of the Chirp in different time and frequency scale, i-iii represent note type-e, -a and –b, respectively.

notes; note-c, 3.0kHz, 2 notes; note-d, 3.0-3.1 kHz, 1 note; and note-e, 3.8-4.1kHz, 5-11 notes. The presence of note-e gave the "buzzing hiss" quality to this display. This display was delivered from a hunched posture, like the Chatter, during times of peak colony activity (Table 3.3). It sounded like "*Tchhht-tschhht-tschhht....* ".

Display type c (LeD-c; Figure 3.7B; **Chirp**). This relatively uncommon display was delivered as a brief tremulous call with variable composition of note types. The display duration was ~1 s with note-a to –d. Display structure was well defined, with note-a and –b in the introduction, note-a to -c in the middle, and note-b in the terminal parts (Figure 3.7B,D). Some Chirps began with note-c and ended with note-d. The frequency and the organization of note types were: note-a, 2.4-3.4 kHz, 0-50 notes; note-b, 2.6-3.3 kHz, 0-18 notes; note-c, 3.1-3.4 kHz, 0-16 notes; and note-d, 3.2 kHz, 0-1 notes (Table 3.2). This display was delivered in the colony or as a flight call when birds departed from the colony (Table 3.3). It sounded like "*scht*" or "*scht.. schiit*".

Display type d (LeD-d; Figure 3.7A; **Chirr-buzz**) was a short (duration 0.3-0.5 s; Table 3.2) and relatively simple display. It was characterized by the presence of a single note type (note-e), short duration and lack of organized introductory, middle, and terminal parts (Figure 3.7A). Note-e was delivered singly as Chirr-buzz at ~3.2-4.1 kHz by birds disturbed by an intruding predator (Table 3.3). It sounded like a rasping, descending "*whisssssst*".

3.5. DISCUSSION

Facial plumage and colourful bills of breeding auklets are specialized as complex visual ornaments (Jones 1999). Here I found comparable diversity and complexity in auklet vocalizations. Both visual and vocal displays are used extensively in sexual and agonistic contexts, and likely have been shaped by sexual and other social sources of selection. Sexually selected displays can evolve rapidly (Masters 2007), so can be particularly sensitive indicators of low-level divergence, such as between conspecific populations or related species. Furthermore display evolution may be more conservative than generally thought (Wenzel 1992), and vocal evolution in Charadriiformes may be particularly conservative (Miller 1996). Higher-level relationships also may be revealed through analysis of multiple displays, an approach I followed in this study.

3.5.1. Repertoire size and composition

A descriptive catalog of display types may be a poor approximation to a species' repertoire, because variations within named display classes may serve as functionally different signals (Hailman and Ficken 1996). Nevertheless, quantitative description is an essential starting point. Repertoire structure was similar across auklet species: the basic vocal units (i.e., note types) were arranged in simple but varied configurations to form displays. I conservatively recognized 22 classes of adult vocal displays (that included 28 note types) across species. This was an underestimate for several reasons: I lacked recordings from outside

the breeding season and outside the breeding colony; chick and fledgling vocalizations were not sampled; I could not confirm several previously described vocalizations (Krick and Kreer of Cassin's Auklet: Thoresen 1964; Chuckling and Soft-lure of Least Auklet: Jones 1993b); and displays consisting of single note types were combined.

Number of note types and repertoire size were similar across species: four to nine and three to five, respectively. Whiskered Auklet vocalizations were most diverse, with nine note types and five display types. Qualitatively, vocal structure included pure-tones, pulses, rapid frequency modulations, broadband noise, smoothly rising and declining frequencies, and abrupt changes in frequency. Syntax (non-random patterns of association of note types; Hailman et al. 1985, Sung et al. 1985) was apparent in all species. Acoustic structure also varied greatly in quantitative terms, and was partly related to body size. For example, note duration averaged 15-370 ms in Least Auklet to 45-1250 ms in Parakeet Auklet; display duration averaged 1-3 s in Least Auklet to 4-19 s in Cassin's Auklet; and inter-note intervals averaged 2 ms in Least Auklet to 1010 ms in Parakeet Auklet. Therefore, brief rapidly uttered notes characterized the smallest species. Frequency attributes varied even more, and reflected body size more closely as in some other avian groups (Ryan and Brenowitz 1985, Bretagnolle 1996, Badyaev and Leaf 1997, Bertelli and Tubaro 2002).

3.5.2. Acoustic relationships among auklets

Harmonic structure and FM were similar in repertoires of Cassin's and Parakeet Auklets. For example; Cassin's Auklet's Krreerr-er was structurally similar to Raft Whinny (Figure 3.3D) of Parakeet Auklet. The latter species' Chipping (Figure 3.3A) consisted of an arrangement of short pulses similar to the "*kut-kut*" segments of Cassin's Auklet's Kut-i-eer (Figure 3.2A). Parakeet Auklet's Whinny (Figure 3.3B) was similar to Kut-i-eer of Cassin's Auklet. The structure and FM of Crested Auklet notes and note type composition in displays were closest to those of the Whiskered Auklet, but F_{μ} was in lower harmonics in the former (Tables 3.1-3.2). However, in Trumpet (Figure 3.4B), note-a and -d arranged alternately and repetitively as in Parakeet and Cassin's Auklets. Predominant use of short duration and high-frequency notes, and the presence of sequentially graded note types along the display made Whiskered Auklet displays (WhD-a to –c) similar to those of the Least Auklet (LeD-a to –b). The latter species' Deep Chatter (Figure 3.6B) was structurally analogous to the Cassin's Auklet Kut-reeah (Figure 3.2D), however. Chirr-buzz (Figure 3.7A) differed from all other displays, but was spectrographically similar to hooting of the Crested Auklet (Figure 3.4E).

I identified two groups based on syntactical arrangement of note types: (1) alternate-note arrangement in Cassin's and Parakeet Auklets; and (2) arrangement of sequentially graded note types through the display in Whiskered and Least Auklets. The alternate arrangement of notes occurs in synchrony with a rhythmic,

slow rocking of the head, so might correspond to inhalation and exhalation. The vocalizing bird moves the head rapidly and asynchronously with respect to the temporal patterning of notes in the group (2). Crested Auklet mainly fell in group (2) however, it lacked rapid head movements, and in Trumpet, two note types (note-a and -d) arranged alternately and with contrasting differences in F_{μ}, which is characteristic of group (1). Crested Auklet Trumpeting was unique among auklet vocal displays for its accompanying postural display including inflation of esophagus or air sacs in the neck region (Jones 1993a).

Repertoires of Cassin's and Parakeet Auklets were the most similar: alternate and repeated arrangement of several notes; presence of broadband noise; contrasting harmonic and frequency differences between note types; prevalence of brief pulses; and duetting. Cassin's Auklet Kut-i-eer and Kreerr-er displays were likely homologous to Whinny and Raft Whinny of the Parakeet Auklet, respectively, even though they occurred in different contexts (Table 3.3). Introductions of some Cassin's Auklet Kut-i-eer calls were long and had brief pulses hence resembled Chipping of the Parakeet Auklet. Crested, Least and Whiskered Auklet repertoires were characterized by sequential gradation of the complexity of notes, predominant expression of trills, and absence of broadband noise. Notes of Whiskered and Crested Auklets were very similar (Figures 3.4-3.5). The Least Auklet repertoire was most similar to that of the Whiskered Auklet. Hence this vocal comparison suggest that relationships might be closer than those currently recognized phylogenetic affinities between Cassin's and

Parakeet Auklets, and between Whiskered and Crested Auklets. The latter two species share similar forehead crests and plumage odor that likely reflect a close phylogenetic relationship (Byrd and Williams 1993, Jones 1993a).

3.5.3. Acoustic relationships of auklets with other alcids

Most studies have identified six tribes in the family Alcidae: Alcini (murres and allies); Cephini (guillemots); Brachyramphini (brachyramphine murrelets); Synthliboramphini (synthliboramphine murrelets); Fraterculini (puffins and Rhinoceros Auklet); and Aethiini, with the more ornamented Fraterculini and Aethini either placed together in a separate clade (Friesen et. al 1996, Pereira and Baker 2008) or considered to be basal (Strouch 1985, Moum et al. 1994, Thomas et al. 2004). Vocal homologies (Miller 1996) were evident in sound note composition and FM of Rhinoceros Auklet (*Cerorhinca monocerata,* Fraterculini) and Aethiini (Gaston and Dechesne 1996). However, F_0 and F_μ were lower in the former (Gaston and Dechesne 1996, Gaston and Jones 1998), possibly due to its greater body size. Compared to Aethiini, Fraterculini has soft calls, simple FM, and lacks compound calls comprising multiple note types (Cramp 1985, Gaston and Dechesne 1996, Gaston and Jones 1998, Lowther et al. 2002, Piatt and Kitaysky 2002a, 2002b). Therefore, visual communication might play a greater role and the simple calls have been selected for short-range communication in Fraterculini.

Repertoires of other distantly related and less ornamented tribes showed fewer homologies with auklet vocalization. Guillemot (*Cepphus*) vocalizations are mainly long, whistle-like notes, likely adapted to long-range communication (Nelson 1985, Butler and Buckley 2002). However, their gradual increase in complexity in FM along the display is similar to Least and Whiskered Auklets. Both species of murres (*Uria*) and Razorbill (*Alca*) in Alcini have brief, low-frequency guttural growls used for short-range communication (Cramp 1985, Gaston and Jones 1998, Lefevre et al. 2001). Compared to auklets, their displays have a simple arrangement of notes, but the FM and amplitude variation of notes are complex and have lower F_0 and F_μ. An exception is the Dovekie (*Alle alle*), whose calls are strikingly similar to those of auklets in F_0, F_μ, FM, sound note arrangement, and use of long-range high intensity display in the colony (Ferdinand 1969, Cramp 1985, Jones et al. 2002). Notes are arranged like those of auklets in all (six) described display types (Ferdinand 1969). Note duration varies from 10-1000 ms, most note types are harmonically rich, F_μ is at 1.5-3.0 kHz, and FM is ~1.0 kHz. Display duration is variable (0.1-4 s), with 1-4 note types per display, and displays were delivered on breeding grounds, in air and at sea, accompanied by distinct postural and flight displays (Ferdinand 1969). Dovekie sound note arrangement is similar to the Least and Whiskered Auklet vocal group. Quantitative vocal comparison of auklets and Dovekie should reveal further evidence for convergence (Jones et al. 2002) between these smallest and distantly related alcids (divergence ~55 Mya; Pereira and Baker 2008).

3.5.4. Effects of environmental and social selection on vocalization

Nocturnal colony attendance supposedly led to complex acoustic communication such as complexity in frequency and amplitude modulation, syntax, presence of complex broadband sounds, and larger repertoires in Alcidae (Jones et al. 1987, 1989a, Drost and Lewis 1995, Nelson 1997, Dechesne 1998). I have not seen such adaptations in nocturnal auklets. The greater repertoire size of the Whiskered Auklet could be an adaptation for its nocturnal colony attendance behavior; however, vocal repertoires of Cassin's and Whiskered Auklets differ little from their diurnal relatives.

I did not study functionality in detail, but this has been commented on by many observers (Manuwal and Thoresen 1993; Jones 1993a, b; Byrd and Williams 1993; Jones et al. 2001). The consistent occurrence of vocal display in different other behavioral context suggests that these repertoires serve basic social functions (Table 3.3). At least a few vocalizations differ between the sexes (e.g., Chatter and Trumpet). The diverse visual ornamentation of *Aethia* has resulted partly from sexual selection (Jones and Hunter 1993, Jones and Hunter 1998, Jones 1999, Jones and Hunter 1999). Vocal traits also might have evolved partly due to sexual selection as many of these displays are used as part of courtship display and in agonistic encounters (Table 3.3). In addition, all auklets except Cassin's Auklet vocalize intensely in rafts and on the sea near colonies, where copulation exclusively takes place (Hunter and Jones 1999, Jones 1999).

Many seabird populations have been decimated by the introduction of alien predators to their breeding islands, and the Aethiini are no exception (Gaston and Jones 1998). Seabird restoration efforts in general, have included removing predators from islands, and enhancing recolonization through habitat restoration and call-playback to attract prospecting birds (e.g., Kress 1997, Miskelly and Taylor 2004). Advertisement displays, such as some vocal displays of breeding auklets at the colony site (Table 3.3) are adapted for long-distance transmission, and are audible over long distances (Wiley and Richards 1982, Endler 1993b); hence they are good candidates for such playback efforts. Use of playback calls for nocturnal seabirds may be especially effective, because most such species are highly vocal and use loud, long-distance calls in intraspecific communication (Bretagnolle 1996). In Aethiini, this is likely to apply to nocturnal Cassin's and Whiskered Auklets. Playback of Kut-reearh, Staccato and Metalic Beedoo displays (Table 3.3) may be useful for future island restoration programs. Raft and Duet Whinny displays of diurnal (some times crepuscular) Parakeet Auklet might also be useful in conditions of poor visibility (e.g., fog), which is prevalent in its breeding range.

3.6. ACKNOWLEDGEMENTS

I thank J. C. Williams and G. V. Byrd for logistic support and permission to conduct research in the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge. I am especially grateful for the Macaulay Library of the Cornell

Lab of Ornithology for providing some of the recording equipment and technical assistance, G. W. Humphries for the assistance in the field and the captain and crew of the vessel M/V Tiglax for transportation to Egg and Buldir Islands. C. E. Braun and two anonymous reviewers provide constructive feedback to the manuscript. Major funding for this study was provided by Natural Sciences and Engineering Research Council Canada - Discovery Grant held by I. L. Jones.

CHAPTER FOUR

ORIGIN AND MAINTENANCE OF MECHANOSENSORY FEATHER ORNAMENTS

4.1. ABSTRACT

Mechanosensory use is a seldom mentioned function for feather ornaments, yet recent experimental evidence showed that the elaborate facial plumes of Whiskered Auklets (*Aethia pygmaea*) have just such a sensory role (Chapter Two). In this study I further explored mechanosensory function of feather ornaments by tracing its phylogenetic pattern among several closely related auklet species (*Aethia*), a group of sexually monomorphic crevice dwelling seabirds. In a maze experiment, Crested Auklets showed an increase in head bumps (262%, $p<0.0001$) under the cancellation of their forehead crest, and a positive correlation of the natural crest length with the frequency of head bumps. However, when an artificial forehead crest was presented, naturally crestless Least Auklets neither showed reduction in head bumps nor any correlation with the head bumps and the length of the attached crest. Only the ornamented younger auklet species that breed in deep crevices appear to have the mechanosensory ability. A pairwise analysis across all non-passerine birds revealed a greater frequency of elongated facial plumes in birds that live in complex habitats and active at low light conditions, suggesting a similar but widespread occurrence for these mechanosensory traits. I was unable to pinpoint the origin of these traits, but the selective pressure enforced by habitat may trigger facial feather exaggeration for mechanosensory use. Once the primordial sensory structures evolved, sexual and

other social selection processes may have acted on these traits and led towards further exaggeration.

4.2. INTRODUCTION

Bird feathers are complex integumentary derivatives specialized primarily for flight, thermoregulation, and maintenance of streamlined body shape (Lucus and Stettenheim 1972, Spearman and Hardy 1985, Clark 2004). However, feathers have many secondary functions, including crypsis (Baker and Parker 1979), optical signaling for mate attraction (Andersson 1994), information about age, sex or individual identity (Whitfield 1987, Dale 2000), mechanical protection (Conover and Miller 1980), and when shed as nesting material (Hansell 2000). Mechanosensory use is another secondary function described recently (Seneviratne and Jones 2008). The Whiskered Auklet (*Aethia pygmaea*), a nocturnal, crevice-dwelling seabird of the North Pacific, uses its long forward-curving forehead crest and long facial plumes as tactile devices to navigate inside their underground rock crevices (Seneviratne and Jones 2008). The forehead crest is derived from contour feathers (Konyukhov 2001) like most feather ornaments (Andersson 1994). The long facial plumes are derived from filoplumes (Konyukhov 2001), which are the specialized sensory feathers in birds used to aid in flight, diving, and general plumage maintenance (Stettenhaim 1972, Gottschaldt 1985, Clark and Cruz 1989, Clark 2004). Another specialized feather type is the semibristle (not present in Alcids), which is mainly found in the face

and is associated with sensory receptors (Küster 1905, Schildmatcher 1931, Lucas and Stettenheim 1972); however, sensory function has not been documented (Ledderer 1972, Conover and Miller 1980, Jackson 2003).

Sexual selection is the main explanation for the evolution of elaborate feather adornments (Darwin 1871, Andersson 1994). Such traits may be favored in mate choice for several reasons (Fisher 1958, Hamilton and Zuk 1982, Basolo 1990, Kirkpatrick and Ryan 1991, see Chapter Two). However, sexual selection may not apply to all examples of feather ornaments, for example, the forward curving forehead crest of New World quails *Callipepla* (Hagalin and Ligon 2001, Parker et al. 2005). Multiple selective forces including both natural and sexual selection can act on ornamental traits leading to change in the original function (Brooks and Endler 2001, Wiens 2001, Takahashi et al. 2008) or for functions other than the mate attraction (e.g. Barn Swallow [*Hirundo rustica*]; Møller 1991, Rowe et al. 2001, Kleven et al. 2006). A natural selection for mechanosensory function could thus explain the enigmatic feather structures of a wide range of birds, not just the Whiskered Auklet crest (Küster 1905, Seneviratne and Jones 2008). A comparative approach examining the occurrence of facial feather appendages in birds and their co-occurrence with habitat preferences provides the best opportunity to test this suggestion. Complex habitats (when open spaces are encroached upon by solid surfaces; Gibson 1998) could pose significant challenges to birds, where vision is the primary navigational aid. Vision provides the feedback stimulation for the control and guidance of locomotion behavior

(Gibson 1998). In low light conditions animals stop locomotion, or use alternate strategies to overcome those limitations (Fenton 1990, Martin 1990, Brigham et al. 1997, Gibson 1998, Brooks et al. 1999). Such strategies can alter physiology, behavior as well as morphology (Krebs et al. 1989, Jacobs et al. 1990, Garamszegi et al. 2001, Martin et al. 2004). Relationships of wing morphology, physiology and behavior in bats to complex habitats have been well explored (Fenton 1990, Neuweiler 1989, Harvey and Krebs 1990, Norberg and Rayner 1987, Safi and Dechmann 2005), but such information is scarce for birds. However, Swaddle and Witter (1998) demonstrated that complex habitats tend to increase symmetry in flight feathers in starlings (*Sturnus vulgaris*).

Auklet (Aethiini, Alcidae) facial ornamentation includes conspicuous white facial plumes and curved forehead-crests, with experimental evidence suggesting a role of both sexual selection (Crested Auklet [*Aethia cristatella*]; Jones and Hunter 1993, 1999, Jones 1999) and natural selection (Whiskered Auklet; Seneviratne and Jones 2008). In the crestless Least Auklets (*A. pusilla*), a mating preference for an artificially attached crest has been found (Jones and Hunter 1998). In *Aethia,* less ornamented Least Auklet is basal to the ornamented Crested and Whiskered Auklets (Pereira and Baker 2008).

Here I tested for mechanosensory ability of crest ornaments in Crested and Least Auklets in a lightproof maze, (which is similar in their breeding crevices). I also used a broader comparative approach to examine the relationships of habitat complexity to facial ornaments in other non-passerine bird families, to determine

how ecological factors influence plumage elaboration. I hypothesized that if the mechanosensory ability of facial plumes in the Whiskered Auklet has been shaped by environmental factors then: (1) the closely related Crested Auklet that shares a similar phylogenetic past and breeding habitat should use the crest similarly, (2) when given an artificial crest, naturally crestless Least Auklets do not show similar tactile use due to the presumed absence of nerve innervations and of associated behavior; thus the Least Auklet served as a natural control, and 3) elongated facial plumes are more likely to evolve in birds that inhabit complex habitats and low light conditions. To test these ideas I recorded exploratory behavior of the subjects under near-infrared illumination inside an experimental chamber similar to that used in a previous study (Seneviratne and Jones 2008, Chapter Two), followed by a pairwise comparison across non-passerine families.

4.3. METHODS

4.3.1. Comparison of the mechanosensory use of elongated plumes in *Aethia*

Field experiments were undertaken at Buldir Island in the western Aleutian Islands, Alaska, USA (52°22'N, 175°54'E) during May to July 2007 (the incubation phase of breeding season for all auklet species). Birds were captured using eight 0.3 m X 0.3 m noose carpets placed on the selected location at Main Talus (the main auklet colony in Buldir Island; Byrd and Day 1986) similar to the methods of Jones (1990) and Jones et al. (2000). The colony consists of large number of auklets of both species, and this trapping method appeared to capture

birds more or less randomly (Jones et al. 2004b). Captured birds were held separately in separate cloth bags before being introduced to the experimental chamber.

4.3.1.1. Experimental setup

I used the same three-chambered maze design of Seneviratne and Jones (2008, Chapter Two), to quantify birds' ability to avoid obstacles in the absence of visual clues. The internal dimensions of the mazes differed, however, to accommodate differences in the body size of Crested and Least Auklets: lightproof test chambers were 9 (height) x 30 x 35 cm for Least Auklets and 13 x 40 x 46 cm for Crested Auklets. Two 2 x 8 x 8 cm wooden panels were attached to the roof as barriers for Least Auklet's; dimensions were 2 x 14 x 14 cm for Crested Auklet's. The entranceway (10 x 10 x 10 cm) connected the 20 x 20 x 20 cm holding pen to the test chamber in both setups. A Sony DCR-DVD308 (Sony Corporation, Japan) camcorder with built-in infrared light-emitting diode (peak wavelength 850 nm) recorded the subjects' behavior through a front window of the test chamber. I used the camcorder's 'Niteshot plus' mode (Sony Handycam Oparating Guide), which allowed recording under near-infrared illumination with greater sensitivity to longer wavelengths (peak spectral sensitivity 800 nm). Seneviratne and Jones (2008) provided the rationale behind for the use of infrared light, and on spectral sensitivity of auklet vision.

4.3.1.2. Treatment exposure

Both species (n = 70) were exposed to three treatments: ornament manipulation, control, and sham, in a balanced random order. The procedure of exposures for the Crested Auklet was similar to those for Whiskered Auklets (Seneviratne and Jones 2008; Chapter Two). Three pieces of 15 x 2 mm black one-sided tape were used to tape down the forward curving crest to the back of the head in the ornament manipulation treatment (cancellation of the elongated plumes). Auklets cannot actively move their crests, and in the wild these crest feathers are bent, and lie flat on the crown feathers in flight and underwater diving (Jones 1993, Gaston and Jones 1998). Hence, bending these flexible feathers was unlikely to cause mechanical stress or cause pain or irritation (Seneviratne and Jones 2008). In the control treatment, test birds were exposed to the maze with no treatment. In sham, tapes were attached similar to the manipulative treatment but the ornament left unaltered (Chapter Two), was introduced to test for the effect of stress caused by handling and irritation as a result of the attached tapes.

Least Auklets were treated similarly, with several differences. In plumage manipulation, an artificial crest (two Crested Auklet crest feathers) was glued to the forehead to resemble the crest of a Whiskered Auklet. Attached crest length varied from 12.8 – 42.1 mm (mean 28.6 mm). The bases of the two feathers were dipped in a small amount of Cyanoacrylate ('Superglue') and placed on the forehead with forceps. The glue dried instantly, therefore, the bird was available

immediately for the exposure. The control was the unmanipulated bird and in sham, only the feather bases with the glue base were attached to the forehead.

For both species, each bird was subjected to all the above treatments once, in a sequential (constrained random) order in all possible combinations; MCS, MSC, CMS, CSM, SMC, SCM (M = manipulation, C = control, S = sham), e.g., bird n_1 was exposed to MCS, n_2 to MSC etc. The order of exposure of subsequent treatments was chosen in a constrained random order, to reduce the carryover effect due to repeated exposure (Neter et al. 1996). Birds were kept in the holding pen for acclimation prior to each exposure, and allowed to walk from the pen to the test chamber. When the bird entered the test chamber its exploratory behavior was video recorded for ~2 min (Seneviratne and Jones 2008). After each exposure, the subject was removed from the maze, switched to the next treatment and immediately reintroduced to the holding pen for the next exposure. Digital video recordings were uploaded to a computer and later I reviewed the recordings and counted the frequency of head bumps (number of head touches on the roof and the walls per minute) crest contacts and beak contacts (similar to the other counts). The definitions of unambiguous 'head bump', 'crest contact' and 'beak contact' were established prior to the counts (rationale for the scoring was given in Seneviratne and Jones 2008). In order to test the repeatability of my scoring, part of the dataset (recordings of all three exposures of 14 Crested and 14 Least Auklets) was scored by an observer who did not have experience in behavioral ecology; it produced similar scores (sign test $p = 0.062$).

4.3.1.3. Feather measurements

Birds were color-banded with plastic leg bands prior to release, to avoid retesting them in the event of recapture. The length of crest plumes (including the artificially placed crest in Least Auklets) was measured with dial calipers (to ± 0.02 mm; Jones et al. 2000). I recorded the number of long crest feathers on Crested Auklets, and the extent of the area of white forehead plumes of Least Auklets from measuring the length of the anteriormost part of the patch of feathers, to the tip of the longest plume. Height of the bill knob, belly colour and age were also noted (Jones and Montgomerie 1992); sex of Crested Auklets was determined following Jones (1993a). All birds were released unharmed near the capture site, 30-120 min after their capture.

4.3.2. Phylogenetic comparison

A phylogenetic comparison across all non-passerine birds was undertaken to determine the relationship of elongated facial feathers to complex habitat and nocturnality. Illustrations from del Hoyo et al. (1992-2002) were used as reference material. I defined 'facial area' (Figure 4.1) to describe presence or absence of long facial plumes. Using lateral view of the head of each species, a straight line was drawn from the proximal-ventral edge of lower mandible to the centre of the eye, and extended across the back of the head; another line was drawn through the centre of the eye at right angle to the first line, defining facial

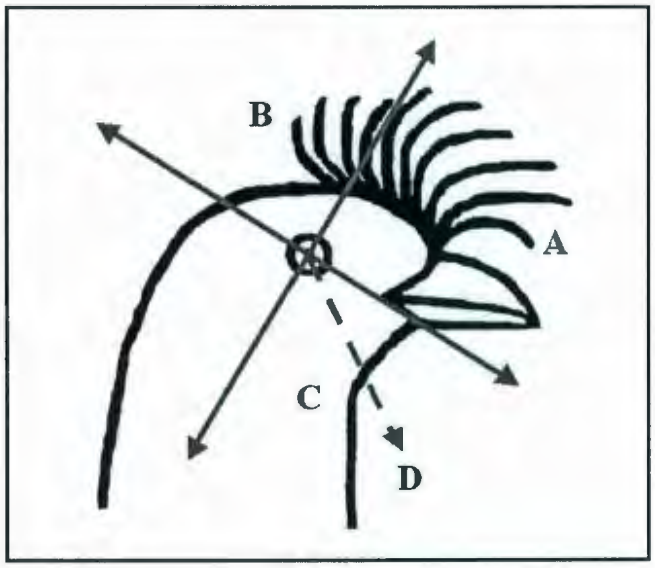

Figure 4.1

Definition of 'facial area' in non-passerine birds as used in comparative analysis. Regions A-D were considered as facial area. The area projecting laterally to either side of the regions A-C (sides of the face) is considered as region D.

regions A, B, and C (Figure 4.1). Laterally projecting plumes projected into region D. A subjective judgment was made to define 'facial region' for species groups that the eyes are situated either closer to the base of the beak (e.g. Pelecaniformes), or towards back of the head (e.g. Cuculidae). Similarly, due to the broad base of the beak of cockatoos (Cacatuidae) and Hornbills (Bucerotidae), the line was drawn from the gape to the pupil. I adjusted these regions for owls (Strigiformes), which usually were shown in frontal aspect. All 27 non-passerine orders (del Hoyo et al. 2002, Clements 2007) were considered for the dataset. I excluded songbirds (Passeriformes) to avoid large numbers of closely related species (Clements 2007). Families that had at least a single species with long facial plumes were included, based on the color illustrations of del Hoyo et al., volumes 1-7 (1992- 2002). Presence/absence of elongated feathers in region A-D, habitat (4 categories; open forest, dense forest, open ground, and dense ground), type of nest (2 categories; open and cavity), and daily activity (2 categories; diurnal and nocturnal) were noted for all species in the families using data from del Hoyo et al. (1992-2002). I scored the facial feather expression blind to the other variables for each member using color illustrations of del Hoyo et al. (1992-2002). The other variables were later noted from the species descriptions blind to the level of facial ornamentation. Therefore, the scoring was an unbiased double blind.

With the *a priori* expectation that elongated plumes would have mechanosensory function in some species, species pairs were constructed by matching ornamented taxa to their most closely related non-ornamented taxa (Whitfield and Tomkovich 1996). Pairs were isolated from the distal and shortest branches of the phylogenetic tree to ensure that they share relatively similar phylogenetic and ecological pasts (Pagel and Harvey 1988, Oakes 1992, Ridley and Grafen 1996), and to minimize errors of incomplete or incorrect phylogenies (Møller and Birkhead 1992). To reduce the phylogenetic dependence of species pairs, a single pair was chosen from each of the distinct clades hence no two pairs share similar branches in the phylogeny (Harvey and Pagel 1991, Ridley and Grafen 1996). Species pairs were based on the most recent phylogenies available for each family; however, preference was given to molecular phylogenies when selecting phylogenetic trees, because facial ornaments can also be included as phenotypic characters for classification. The following phylogenies were used: Sibley and Ahlquist 1990, Mariaux and Braun 1996, Livezey 1997, van Tuinen et al. 1998, Brown and Toft 1999, Hughes and Baker 1999, Johnson and Clayton 2000, Kennedy et al. 2000, Veron and Winney 2000, Kirchman et al. 2001, Bush and Strobeck 2003, Dumbacher et al. 2003, Dyke et al. 2003, Ryu and Park 2003, Bertelli and Porzecanski 2004, Moyle 2004, Overton and Rhoads 2004, Pereira and Baker 2004, Marks and Willard 2005, Moyle 2005, Thomassen et al. 2005, Webb and Moore 2005, Barrowclough et al. 2006, Benz et al. 2006, Bertelli et al.

2006, Crowe et al. 2006, Larsen et al. 2007, Livezey and Zusi 2007, McGuire et al. 2007, and Pereira and Baker 2008.

I made the following alterations to the dataset to accommodate the diverse phylogenetic, morphological, and behavioral variability of non-passerines. Species from the same genus were considered to be more closely related than species from different genera, unless otherwise supported by phylogeny. When more than two candidate species pairs were available for a clade, the first pair in the checklist of Clements (2007) was selected. When there were multiple species with the same characters, only one representative species was chosen. When the most recent phylogeny did not provide necessary resolution for a given clade, an older phylogeny was used to revise the recent one, as long as they did not disagree substantially. Groups that lacked a closely related species for comparison (e.g. *Gaura* – crowned pigeons) or with an ambiguous phylogenetic position (e.g. tree swifts; Hemiprocnidae) were eliminated. Overall, crowned pigeons, owlet-nightjars (Aegothelidae), Hoatzin (Opisthocomidae), frogmouths (Podargidae), tree swifts, todies (Todidae), motmots (Momotidae), and puffbirds (Bucconidae) were excluded. Further, Megapodiidae (megapods), Accipitridae (hawks and eagles), Balearicinae (crowned cranes), Vanellinae (Lapwings), were excluded, as the crest is projected towards the nape. Woodpeckers (Picinae), include many similarly ornamented species, but only typical Asian woodpeckers (Picini) were included as a monophyletic representative group.

4.3.3. Analysis

I used Minitab Release 13.31 (Minitab Inc., State College, Pennsylvania, USA) and SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA) for the statistical analysis. In the maze experiment, habituation to the maze and the cumulative effect of stress due to repeated handling and manipulations were collectively tested using the order of exposure in general linear model (as two-way ANOVA) by keeping both the treatment (M, C, S) and the order of exposure (M--, -M-, --M; C--, -C-, --C; S--, -S-, --S) fixed (Sokal and Rohlf 1995). The frequency of head bumps, crest contacts and beak contacts under different experimental treatments were compared using two-way ANOVA – randomized blocks (Sokal and Rohlf 1995) as described elsewhere (Seneviratne and Jones 2008). Residuals were checked for normality, homogeneity, and independent errors. General linear model (regression; Sokal and Rohlf 1995) was used to determine the relationships of crest length to the ability to deal with the maze under the manipulative treatment. No significant deviation of residuals from normality, and errors were homogenous and independent. Chi-square comparisons were carried out in SAS 9.1.3 to determine relationships between presence/absence of long facial plumes to habitat type, daily activity, and nest type). I used SAS GENMOD procedure with Poisson distribution and log-link function (considering type 1 and type 3 analyses). Statistical significance of all above tests was reached at $\alpha = 0.05$.

This study was conducted under the approval of the Animal Care Committee of the Memorial University of Newfoundland (protocol number 07-

13-IJ and 07-14-IJ). Throughout the study, recommendations of the Canadian Council on Animal Care (CCAC) and the Animal Behavior Society guidelines for the use of animals in research were strictly followed.

4.4. RESULTS

For Crested Auklets, there was a reduction of activity from second to third exposure (two-way ANOVA, $F_{2,204} = 6.92$, $p = 0.001$); hence, the third exposure of birds to the maze apparatus was excluded from further analysis. For the first two exposures, Crested Auklets showed more head bumps in the plumage manipulative treatment relative to the control (262%, $p < 0.0001$;Tables 4.1-4.2; Figure 4.2). Control and sham treatments did not differ in mean frequency of head bumps and feather ornament contacts (Tables 4.1, 4.2). However, the frequency of contact of the crest with the ceiling and walls of the maze was higher in the control and sham birds (Table 4.1). Crest length of the Crested Auklet (mean 35.7[± 7.3 SD] mm) was positively correlated with the frequency of head bumps in the manipulation (Tables 4.1, 4.2; Figure 4.3). Crest length was also positively related to the number of crest feathers (Table 4.2). Other relationships were not significant including the sex (head bumps with respect to the sex; two-way ANOVA; $F_{1, 132} = 2.66$, $p = 0.105$). In Least Auklets the artificial crest had no influence on head bumps (Tables 4.1-4.2; Figure 4.2-4.3). Similarly, head bumps and beak contacts between control and sham did not differ (Tables 4.2-4.3), suggesting that the stress caused by the glue base and feather bases

Table 4.1

Crested and Least Auklets' performance inside the experimental maze.

	Crested Auklet			Least Auklet		
Variable	Mean (number of hits/min)	SEM	n	Mean (number of hits/min)	SEM	n
(a) Head bumps						
Manipulation	5.35	0.44	69	2.72	0.28	69
Control	2.04	0.26	69	3.00	0.24	70
Sham	1.74	0.21	69	2.81	0.29	70
(b) Crest hits						
Manipulation	-	-	-	6.85	0.54	69
Control	6.63	0.43	69	-	-	-
Sham	6.26	0.54	69	-	-	-
(c) Total hits						
Manipulation	5.35	0.44	69	9.57	0.77	69
Control	8.67	0.62	69	3.00	0.24	70
Sham	8.01	0.70	69	2.81	0.29	70
(d) Beak touches						
Manipulation	5.83	0.53	69	4.15	0.66	69
Control	3.52	0.40	69	4.93	0.68	70
Sham	3.86	0.51	69	5.67	0.79	70

Table 4.2

Effect of different treatment exposures on Crested and Least Auklets, and their relationship with the size of some of the ornaments.

	Crested Auklet				**Least Auklet**			
Variable	***F***	**df**	***p***	***R^2***	***F***	**df**	***p***	***R^2***
Head bumps in manipulation	32.24	2,67	<0.001	-	1.14	2,134	0.322	-
Head bumps b/w control and sham	0.13	1,67	0.715	-	1.16	1,67	0.284	-
Crest hits b/w control and sham	0.42	1,67	0.521	-	-	-	-	-
Beak contacts in manipulation	4.52	2,132	0.013	-	5.27	2,134	0.006	-
Correlation with crest length								
Head bumps in manipulation	4.34	1,66	0.041	0.06	0.13	1,66	0.772	0.01
Crest hits in control*	9.45	1,66	0.003	0.13	4.15	1,61	0.046	0.06
Total hits in control*	6.36	1,66	0.14	0.09	3.39	1,58	0.071	0.06
Beak contacts in manipulation	1.17	1,66	0.283	0.02	0.01	1,66	0.929	0.00

Beak contacts in control	0.90	1,66	0.347	0.01	-	-	-	-
Number of crest feathers	13.18	1,66	0.001	0.17	-	-	-	-
Correlation with head bumps**								
White facial plumes	-	-	-	-	0.00	1,66	0.968	0.00
Bill knob	-	-	-	-	0.37	1,66	0.544	0.00

Two-way ANOVA-randomized blocks and general leaner modal (regression) were used for the analysis (see text).

For Least Auklets these values represent, * manipulation, ** control treatments (see text).

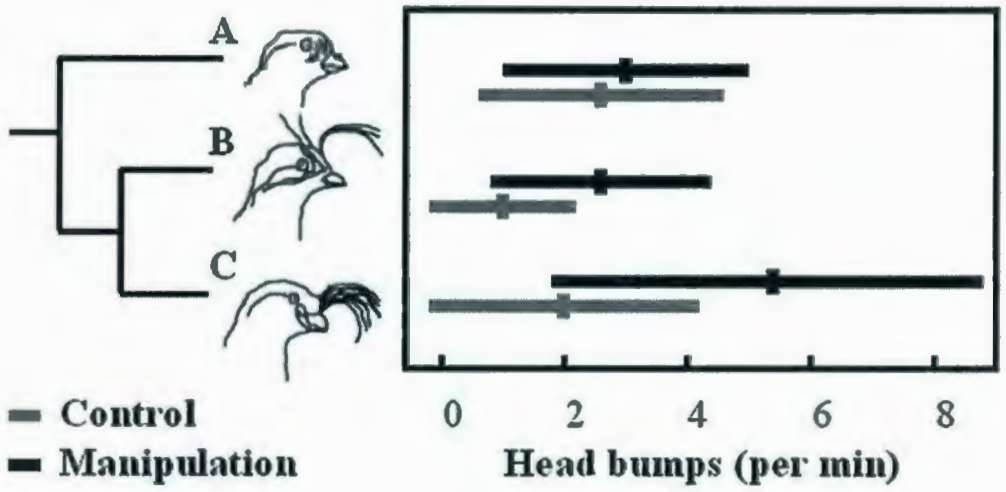

Figure 4.2

The effect of the treatment exposure (control and plumage manipulation) on the frequency of head bumps in three auklet species; (A) Least Auklet (n = 69), (B) Whiskered Auklet (n = 99), (C) Crested Auklet (n = 69). The plumage manipulation represents crest cancellation for Whiskered and Crested Auklets. For naturally crest-less Least Auklets, an artificial crest was provided in plumage manipulation (see text). The filled squares represent the mean frequency of head bumps (±SD). The phylogenetic tree is adopted from Pereira & Baker (2008). Whiskered Auklet data were taken from Seneviratne and Jones (2008).

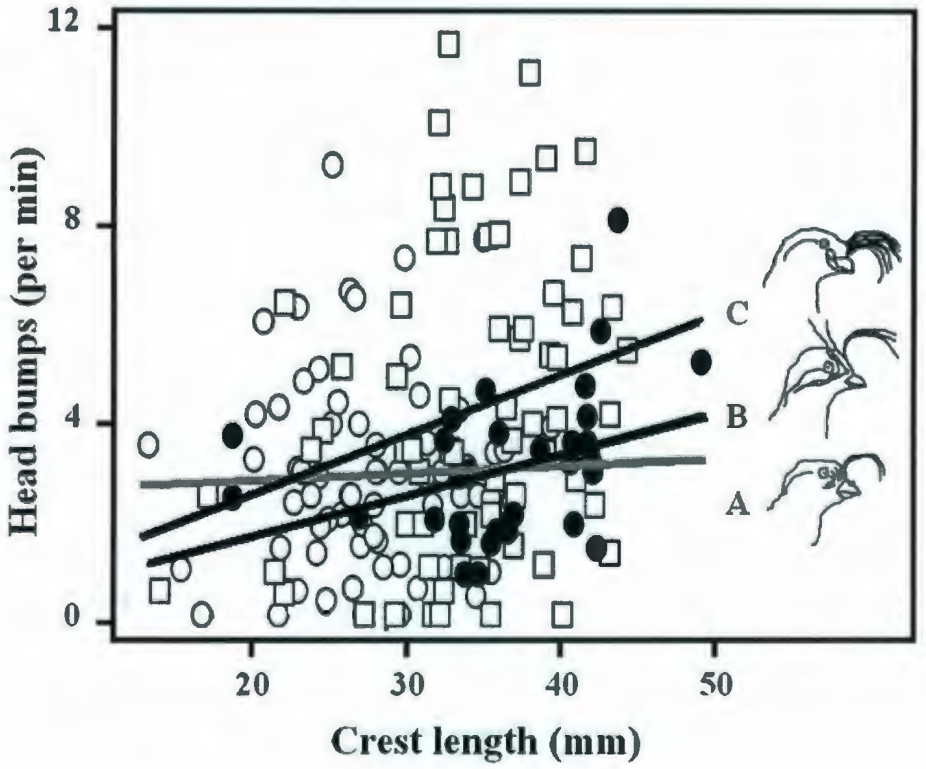

Figure 4.3

Relationship between natural crest length and frequency of head bumps inside the maze under cancellation of the crest. The corresponding trend lines were shown in front of each auklet species (Least, A; Whiskered, B; Crested, C). In Least Auklets the crest was attached as seen in the illustration. Open squares - Crested Auklet (n = 68); open circles – Least Auklets (n = 68); filled circles – Whiskered Auklet (n = 32). Whiskered Auklet data were taken from Seneviratne and Jones (2008).

did not cause a significant change in the behavior. The exploratory behavior of birds was similar across treatments, and crest length was not correlated with head bumps under manipulative treatment (Table 4.2). The frequency of total hits (crest and head, excluding beak contacts) was high in the manipulation (Table 4.1), however, beak hits were reduced in plumage manipulation (Tables 4.1-4.2). Crest length was not correlated with frequency of head bumps in manipulative treatment (Table 4.2). Similarly, there was not any relationship between height of the bill knob and extent of the white facial plumes with frequency of head hits in the control (Table 4.2). In Least Auklet trials the order of exposure was insignificant ($F_{2,202} = 2.47$, $p = 0.087$).

4.4.1. Phylogenetic analysis of facial appendages in non-passerine birds

Elongated facial feathers occur in 33 of 102 total families in 20 orders of non-passerines (of 27 total orders). Of 784 species in these 33 families, I identified 42 species pairs that could be used to compare relationships of facial plumage to habitat, nest type and daily activity patterns (Appendix 4.1). Presence of facial feather ornaments was not related to habitat ($X^2 = 1.79$, $p = 0.62$) or daily activity ($X^2 = 1.10$, $p = 0.29$). However, when I collapsed the four habitat categories (open forest, dense forest, open ground and dense ground) into two (complex habitat versus open habitat; Table 4.3), the presence of elongated plumes was strongly correlated with complex habitat (Table 4.4) and activity at low light conditions.

Table 4.3

The distribution of the members of 42 species pairs of non-passerine birds between habitat type and lighting condition.

Habitat	**Lighting condition**	**Species with long facial plumes**	**Species without long facial plumes**
Open	Diurnal	9	16
	Nocturnal*	2	3
Complex	Diurnal	24	21
	Nocturnal*	7	2

* crepuscular birds were lumped with the nocturnal species.

Table 4.4

The relationship of facial feather ornaments with the habitat and the lighting condition. (a-b) Considering both homogeneous and heterogeneous pairs, (c) considering only heterogeneous pairs separately.

		Chi-Square	**P**
a	Ornament*Habitat	6.37	0.0116
	Ornament*Lighting condition	2.70	0.1001
	Habitat*Lighting condition	0.11	0.7408
b	Ornament*Habitat	11.29	0.0008
	Ornament*Lighting condition	4.68	0.0306
c	Ornament*Habitat	13.33	<0.001
	Ornament*Lighting condition	6.67	0.01

When the ratio of longplume (LP) and nonplume (NP) birds combine accross light conditions, then the ratio of LP-complex to LP-open is 3:1, but NP-complex to NP-open is only 1:1. The ratio of LP to NP birds in open habitats (light condition combined) is 1:2, but LP:NP is 3:2 in complex habitats. Finally, in nocturnal species only, the ratio of LP:NP is 1:1 in open habitats but 3:1 in complex habitats. Elimination of homogeneous pairs (both members of the pair have the same habitat category or have the same activity pattern) from the analysis resulted in stronger correlations (Table 4.4). However, presence of long plumes was not related to nest type ($X^2 = 0.16$, $p = 0.69$).

4.5. DISCUSSION

Here I showed that the environment plays a key general role in the occurrence of mechanosensory function as observed previously in Whiskered Auklets (Seneviratne and Jones 2008). Crested Auklet, like the closely related Whiskered Auklet, bumped into surfaces of the experimental maze more often when the crest was taped down. Furthermore, the number of bumps was positively correlated with crest length of individual birds. Only the younger species of auklets (Whiskered and Crested Auklets, Pereira and Baker 2008) that breed in deep rock crevices express this trait, hence, the mechanosensory capacity apparently has been acquired only in the Crested-Whiskered branch in Aethiini. The Least Auklet breeds in shallow crevices and did not exhibit a similar use of an attached artificial crest, which supports the idea of a later development of the trait and its use. Furthermore, non-significant difference of the frequency of head bumps and artificially attached crest supports my study design; the observed reduction of

head bumps is not a simple physical barrier effect of the long forehead plumes. Expression of elongated facial plumes is rare but widespread in non-passerine birds, and is associated significantly with habitat complexity and lowlight conditions, suggesting that these elongated plumes may have mechanosensory use in other species. Although I was unable to pinpoint the origin or maintenance of this tactile use, the correlation between the habitat characteristics and daily activity pattern suggests that the selective pressure enforced by the habitat could trigger facial feather elongation. Once protruding feathers evolved, sexual selection could explain the elaboration of traits (Jones and Hunter 1993,1999, Andersson 1994), while the use of the feathers for sensing obstructions continued where necessary and could partly explain the highly embellished ornaments of Crested and Whiskered auklets.

If the crest provides mechnosensory aid in underground navigation, why has it not evolved in crevice dwelling Least Auklets? Lack of genetic plasticity to produce the trait (Qvarnstroem et al. 2006, Wright et al. 2008), secondary disappearance due to cost of bearing or random genetic drift (Borgia 1993, Jones and Hunter 1998, Johnson 1999, Wiens 2001), or lack of adequate selection pressure (either natural or social) to initiate the primordial trait (Andersson 1994), could be some of the explanations. The lack of a fully resolved phylogeny for auklets prevents us from determining the origin of the crest. However, all recent phylogenetic hypotheses point to a very close relationship between the Least Auklet and other crest-bearing auklets (Friesen et al. 1996, Thomas et al. 2004,a b, Pereira and Baker 2008, Chapter Five), which contradicts the notion that lack of genetic plasticity could hinder the Least Auklet in produceing the trait. The feather

ornaments of auklets are apparently cheap to produce (Jones and Montgomerie 1992) and maintain (low aerodynamic and hydrodynamic cost; Jones and Hunter 1998), however, the social cost due to the competition of dominant and aggressive sympatric Crested Auklets is less clear (Jones and Hunter 1998). Crested Auklets have a mating preference and status signaling function associated with the crest (Jones and Hunter 1993, 1999), hence, an agonistic pressure from the sympatric Crested Auklet may hinder the expression of the trait in Least Auklets. The latter species' sexual interest in artificially attached crests favors a possibility of a crested common ancestor (Jones and Hunter 1998). Finally, both Crested and Least Auklets are diurnal, and hence possess fewer visual constraints than their nocturnal counterpart. However, of the three species, only Least Auklet uses shallow comparatively better-lit crevices, therefore it might not subjected to stronger selection pressure towards facial feather exaggeration to cope complex underground crevices (Seneviratne and Jones 2008). Taken together, this comparative evidence supports the idea that the deep-crevice nesting behavior may have triggered the facial feather elongation in auklets.

The greater intraspecific variability of auklet crests, and mutual mate attraction for the Least and Crested Auklet facial ornamentation suggests the role of sexual selection in at least the maintenance of these traits (Byrd and Williams 1993, Jones and Hunter 1993, 1999, Jones et al. 2000). However, my work shows that the origin of these traits could have been based on the initial survival advantage gained by a naturally selected mechanosensory capacity (Fisher 1958, Kirkpatrick 1982). Furthermore the Crested Auklet uses its crest as a 'badge of status' (Jones and Hunter 1999), the

mechanosensory capacity would be a 'benefit' that reflects the quality of its bearer; hence the crest could be selected through purely mate choice (Zahavi 1975, Andersson 1994). Most studies used length categories for trait-manipulative experiments (Rowe et al. 2001, Andersson 1982a, Møller et al. 1995), but I kept crest length as a continuous variable in Least Auklet trials to compare it with the natural crests of the other two species. I expected that the shortest crests might have mimicked the precursor of the crest (as used in Rowe et al. [2001] for tail streamers) while the longer crests might have mimicked the fully expressed state, if Least Auklets were to have the crest. However, there was no correlation with the head bumps and either length class. However, another possibility is that the short facial plumes of Least Auklets do have a sensory function, but that my artificial crests simply were too crudely attached (i.e., by gluing) to carry on this function.

Based on my comparative analysis, the positive correlation of habitat complexity and low light conditions with the expression of facial appendages provides the first such clue for a correlated evolution of complex habitat and these feather traits. Birds living in complex habitats such as the canopy of tropical rainforests or grasslands with tall grass, are likely to encounter greater density of objects that they have to avoid either in flight or while moving along the branches or on ground. Low light conditions can cause equal or greater challenges even in open habitats (Hodos 1993, Brooks et al. 1999). Such habitat complexity could force anatomical, physiological and behavioral changes (Fenton 1990, Garamszegi et al. 2001, Mandelik et al. 2003, Safi and Duchmann 2005, Rilov et al. 2007). Feather elongation in the facial region would benefit birds to navigate through dense vegetation or complex habitats that could potentially damage vital organs (e.g. eye,

ear drum) and bare parts (bill, gape, nostril) or even plumage. Further, mechanosensing would likely be useful for exploring novel habitat for food, or nesting chambers for cavity nesting species.

However, caution needs to be taken while grouping broad range of habitats into binary categories of 'complex' and 'open'. The size of the bird could be an important consideration to define its surrounding, as grass or other shorter vegetation would not clutter a tall bird's immediate habitat in a grassland, but it could clutter the surroundings of a smaller ground dwelling bird. Similarly, the height of the bird, density of the forest's understory, the condition of the beach, and general behavior (e.g. tree trunk dwelling in the canopy from flying within the canopy) are some of the other factors needed to be considered when assigning the habitat into fewer categories (complex/open). Diurnal and nocturnal activity patterns are fairly separated hence, the categorization of the daily activity pattern posed a lesser challenge. Spatial memory is another consideration as birds might have maintained a 'memory map' (Gibson 1998) of the special distribution of surrounding objects. This ability would be especially a concern for nest type (cavity/open) as nest owners visit their nest site on a regular basis.

Since I only considered families with facial ornaments, my dataset was not suited for a detailed phylogenetic comparison to identify the origin and maintenance of these traits. The use of complex habitats is widespread in birds hence such a phylogenetic correlation requires a broader phylogeny including all species that live in complex habitats to avoid overrepresentation of ornamented forms (Höglund 1989, Höglund and Sillén-Tullberg 1994). Phylogenetic data tend to be dependent on each other due to the

common ancestry (Harvey and Pagel 1991, Ridley and Grafen 1996), hence independent contrasts (Felsenstein 1985) are widely used to reduce this statistical problem (e.g. Oaks 1990, Garamszegi et al. 2001, Höglund and Sillén-Tullberg 1994). However, to avoid complex (and often unresolved) phylogenies and to accommodate categorical variables, I used pairwise comparisons (Pagel and Harvey 1988, Møller and Birkhead 1992, Ridley and Grafen 1996). My pairwise analysis not only controlled for phylogeny (Møller and Birkhead 1992) but also avoided the pooling fallacy that arises due to common ancestry (Martins and Hansen 1996).

Using a comparative approach, I experimentally demonstrated that both recently evolved auklet species have a mechanosensory use for facial feather ornaments. More widely, the comparative evidence suggests that elongated facial plumes are widespread across non-passerine birds and are more likely to evolve in birds live in complex habitat and active at lowlight conditions. However, future comparative studies need to test the origin and maintenance of this tactile function in the light of a rigorous phylogenetic background, which I have not attempted here. Furthermore, confirmation of mechanosensory use for feather ornaments requires detailed anatomical and physiological study of representative species to investigate extensive innervation or aggregation of mechanoreceptors on or near these feather tracts, which would expected to be more extensive than in other feather ornaments

4.6. ACKNOWLEDGMENTS

I thank C. Small and G. W. Humphries for assistance in the field, G. V. Byrd and J. C. Williams for logistic support and permission to conduct research in the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge (AMNWR), and K. Lewis and D. Schneider for advice in the analysis. The captain and the crew of vessel M/V Tiglax provided the vessel transportation to Buldir Island. I greatly acknowledge the Frank M. Chapman Memorial funds of the American Museum of Natural History and Donald L. Bleitz Research Awards of the American Ornithologist's Union for funding part of this research. Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grant held by I. L. Jones provided rest of the funding.

APPENDIX 4.1

Species representing all non-passerine orders used for the pairwise comparison. The ornamented taxon is given first (in bold text) for each species pair.

Order	Family	Scientific name	English name
Tinamiformes	Tinamidae	***Eudromia formosa***	**Quebracho Crested Tinamou**
		Tinamotis pentlandii	Puna Tinamou
Struthioniformes	Apterygidae, Dromaiidae	***Apteryx australis***	**Southern Brown Kiwi**
		Dromaius novaehollandiea	Emu
Galliformes	Cracidae	***Crax rubra***	**Great Curassow**
		Mitu mitu	Alagoas Curassow
	Numididae	***Guttera pucherani***	**Crested Guineafowl**
		Acryllium vulturinum	Vulturine Guineafowl
	Odontophoridae	***Colinus cristatus***	**Crested Bobwhite**
		Colinus leucopogon	Spot-bellied Bobwhite
	Phasianidae	***Lophophorus impejanus***	**Himalayan Monal**
		Lophophorus sclateri	Sclater's Monal
	Phasianidae	***Lophura ignita***	**Crested Fireback**
		Lophura erythrophthalma	Crestless Fireback
	Phasianidae	***Polyplectron bicalcaratum***	**Grey Peacock-Pheasant**
		Polyplectron germaini	Germain's Peacock-Pheasant
Anseriformes	Anhimidae	***Anhima cornuta***	**Horned Screamer**
		Chauna chavaria	Northern Screamer
Spheniscifformes	Spheniscidae	***Eudyptes pachyrhynchus***	**Fiordland Penguin**
		Megadyptes antipodes	Yellow-eyed Penguin
Pelecaniformes	Phalacrocoracidae	***Phalacrocorax auritus***	**Double-crested Cormorant**
		Phalacrocorax brasilianus	Neotropic Cormorant
		Phalacrocorax purpurascens	**Macquarie Shag**

		Leucocarbo bougainvillii	Guanay Cormorant
Gruiformes	Chariamidae	***Cariama cristata***	**Red-legged Seriema**
		Chunga burmeisteri	Black-legged Seriema
Charadriiformes	Alcidae	***Aethia pygmaea***	**Whiskered Auklet**
		Aethia pusilla	Least Auklet
		Cerorhinca monocerata	**Rhinoceros Auklet**
		Fratercula cirrhata	Tufted Puffin
Columbiformes	Columbidae	***Geophaps plumifera***	**Spinifex Pigeon**
		Geophaps scripta	Squatter Pigeon
Psittaciformes	Cacatuidae	***Cacatua sanguinea***	**Little Corella**
		Cacatua goffiniana	Tanimbar Corella
		Cacatua moluccensis	**Salmón-crested Cockatoo**
		Cacatua alba	White Cockatoo
Cuculiformes	Musophagidae	***Tauraco schalowi***	**Schalow's Turaco**
		Tauraco hartlaubi	Hartlaub's Turaco
		Musophaga rossae	**Ross's Turaco**
		Musophaga violacea	Violet Turaco
		Corythaixoides concolor	**Grey Go-away-bird**
		Corythaixoides personatus	Bare-faced Go-away-bird
Strigiformes	Strigidae	***Xenoglaux loweryi***	**Long-whiskered Owlet**
		Micrathene whitneyi	Elf Owl
		Otus rufescens	**Reddish Scops Owl**
		Otus thilohoffmanni	Serendib Scops Owl
		Megascops asio	**Eastern Screech Owl**
		Megascops flammeolus	Flammulated Owl
		Bubo virginianus	**Great Horned Owl**
		Bubo scandiacus	Snowy Owl
		Strix ocellata	**Mottled Wood Owl**
		Strix leptogrammica	Brown Wood Owl
Caprimulgiformes	Caprimulgidae	***Veles binotatus***	**Brown Nightjar**
		Chordeiles minor	Common Nighthawk

Apodiformes	Trochilidae	***Stephanoxis lalandi***	**Black-breasted Plovercrest**
		Abeillia abeillei	Emerald-chinned Hummingbird
		Popelairia popelairii	**Wire-crested Thorntail**
		Popelairia langsdorffi	Black-bellied Thorntail
Coliiformes	Coliidae	***Colius striatus***	**Speckled Mousebird**
		Colius leucocephalus	White-headed Mousebird
Trogoniformes	Trogonidae	***Pharomachrus mocinno***	**Resplendent Quetzal**
		Pharomachrus fulgidus	White-tipped Quetzal
Coraciiformes	Brachypteraciidae	***Brachypteracias leptosomus***	**Short-legged Ground Roller**
		Coracias garrulous	European Roller
	Alcedinidae	***Megaceryle lugubris***	**Crested Kingfisher**
		Megaceryle maxima	Giant Kingfisher
	Bucerotidae	***Tropicranus albocristatus***	**White-crested Hornbill**
		Tockus camurus	Red-billed Dwarf Hornbill
		Bycanistes cylindricus	**Brown-cheeked Hornbill**
		Bycanistes bucinator	Trumpeter Hornbill
Piciformes	Capitonidae	***Gymnobucco peli***	**Bristle-nosed Barbet**
		Stactolaema leucotis	White-eared Barbet
		Pogoniulus atroflavus	**Red-rumped Tinkerbird**
		Pogoniulus coryphaeus	Western Tinkerbird
		Lybius vieilloti	**Vieillot's Barbet**
		Lybius leucocephalus	White-headed Barbet
		Trachyphonus vaillantii	**Crested Barbet**
		Trachyphonus purpuratus	Yellow-billed Barbet
	Picidae	***Dinopium rafflesii***	**Olive-backed Woodpecker**
		Picus canus	Grey-headed Woodpecker
		Chrysocolaptes festivus	**White-naped Woodpecker**
		Gecinulus grantia	Pale-headed Woodpecker
		Reinwardtipicus validus	**Orange-backed Woodpecker**
		Blythipicus pyrrhotis	Bay Woodpecker

CHAPTER FIVE

EVOLUTION OF VOCALIZATIONS AND THE VOCAL APPARATUS OF AUKLETS (ALCIDAE: TRIBE AETHIINI)

5.1. ABSTRACT

Patterns of vocalization have been studied in phylogenetic and ecological contexts to understand behavioral and signal evolution in birds. In non-oscine birds, unlearned vocalizations are supposed to be informative of phylogenetic affinities. Habitat, signaling context, and morphology can also affect different aspects of a species' vocal repertoire. To test the hypothesis that phylogenetic relationships reflect vocal evolution in auklets (Alcidae, Aethiini), I mapped 28 vocal and 10 syringeal characters onto their molecular phylogeny. Low Consistency and Retention Indices (CI = 0.70, RI = 0.10) indicated a poor fit between molecular- and vocalization derived phylogenies. Temporal and syringeal attributes (note type diversity, note and display duration, syringeal dimensions and degree of calcification) showed a greater congruence with molecular trees than did frequency attributes (harmonic structure, frequency modulation, broad band noise, and trills). A combination of factors including genetic relatedness, social displays (e.g., visual ornaments), and the acoustic properties of the breeding habitat may all have played a role in vocal divergence. Taken together, my results indicated a complex evolutionary pattern in auklet vocalizations, and suggest that vocal and other displays have evolved in tandem, in a close association with species divergence.

5.2. INTRODUCTION

Vocalizations often are sensitive indicators of speciation and population divergence (Lanyon, 1969, Payne 1986, Martens 1996, Isler et al. 2005, 2007), and are used routinely in modern species-level systematics (Cuervo et al. 2005, Athreya 2006, Gonzaga et al. 2007). Similarly, vocal and other behaviors have been studied to elucidate the phylogenetic history of species groups (e.g., Tinbergen 1959, Van Tets 1965, Irwin 1996, Omland and Lanyon 2000). In birds, vocalizations that are not learned are especially likely to be phylogenetically informative, and such vocalizations are widespread as they are characteristic of all species outside Passeriformes, Psittaciformes, and Apodiformes (Nottebohm 1972, Baptista and Schuchmann 1990, Farabaugh and Dooling 1996, Price and Lanyon 2002, Jarvis 2006). Nevertheless, even some oscine (Suborder Passere; true song birds) vocalizations are evolutionarily conservative, and have been used to reconstruct evolutionary histories and determine relationships (Kroodsma and Canady 1985, Payne 1986, Baptista 1996, Päckert et al. 2003).

Vocalizations are, however, under strong selection and many inter-specific similarities may result from convergent adaptations to the physical environment (Morton 1975, Wiley and Richards 1982, Endler 1993b, Badyaev and Leaf 1997, McCracken and Sheldon 1997, Seddon 2005, Boncoraglio and Saino 2007). Acoustic signals vary with the signaling context, thus homoplasy characterizes many kinds of vocalization, such as alarm, aggressive or submissive calls (Marler 1955, Morton 1975). Vocal signals that have evolved for mate attraction, advertisement and intrasexual competition may be subject to strong sexual selection (Andersson 1994, Searcy and Yasukawa 1996, Irwin

2000). Finally, because of the mechanical origin of the vocal signal, certain sound properties can be directly linked to morphology of the syrinx and vocal tract (Bertelli and Tubaro 2002).

Most comparative studies of vocalizations have examined only one or a few acoustically simple display classes (Davis 1962, 1965, Winkler and Short 1978), or lacked a robust phylogenetic framework (Jouventin 1982, Bretagnolle 1996). Comparative analysis of more diverse sets of sound classes for clades with complex vocalizations, large repertoires, and acoustic differentiation across species should be more informative (Catchpole 1982, Irwin 1996, Isler et al. 2007), especially within an explicit phylogenetic framework established by molecular or other data (Price and Lanyon 2002, Päckert et al. 2003, Shelley and Blumstein 2004). Based on comparable information on complete vocal repertoires, I undertook such a study to elucidate the evolution of vocalizations of a tribe of five species of diving seabirds, the auklets (Alcidae, Aethiini).

Auklets were chosen to investigate vocal evolution for several reasons. The group is monophyletic, falls within a well-resolved clade (see Chapter One), and is the result of a rapid adaptive radiation within their planktivore niche accompanied by the evolution of diverse and spectacular feather and bill ornamentation (Jones 1999). Species-level relationships in the genus *Aethia* are not definitively resolved, but it is agreed that the Cassin's Auklet (*Ptychoramphus aleuticus*) is the outgroup to *Aethia* (Strauch 1985, Freisen et al. 1996, Thomas et al. 2004a,b, Pereira and Baker 2008, see Chapter One). All auklets are highly vocal at the breeding colony, and quantitative information on their

vocalization and vocal repertoires is available (Chapter Three). Social behavior is similar across species (Gaston and Jones 1998), and the physical environment at breeding colonies is basically similar, although species differences exist. Colony attendance of most species is diurnal, whereas Cassin's Auklet and Whiskered Auklet (in most of its range) visit the colony only at night (Gaston and Jones 1998). The breeding habitat substrates are variable: Cassin's Auklet breeds exclusively in soft soil in slopes covered with grass and sometimes trees (Thoresen 1964, Manuwal and Thoresen 1993), Crested and Least Auklets exclusively breed in rock crevices (Jones 1993a,b), Whiskered Auklet also prefer rock crevices but sometimes uses soil and grassy slopes (Zubakin and Konyukhov 1999, Hunter et al. 2002), and Parakeet Auklet breeds in all of the above habitat types (Jones et al. 2001).

I analyzed acoustic characters from total repertoires along with syringeal characters to identify correlates with vocal divergence. I hypothesized that phylogenetic relationships were a major determinant of vocal evolution in Aethiini. Hence I predicted that vocalizations and the syrinx of closely related Crested and Whiskered Auklets (Freisen et al. 1996, Pereira and Baker 2008) would be more similar to each other than to those of Least, Parakeet and Cassin's Auklets, and that vocalizations and the syrinx of *Aethia* would differ from those of the Cassin's Auklet. I further anticipated that this comparison would provide insight into the selective forces that have driven species divergence in auklets.

5.3. METHODS

5.3.1. Study sites and acoustic analyses

Audio recordings were made at Buldir Island (52° 22'N, 175° 54'E), and Egg Island (53°52'N, 166°03'W), Aleutian Islands, Alaska, during times of peak colony attendance of each species. Both islands are talus- and grass-covered, treeless, volcanic islands, with large breeding colonies of auklets (Bradstreet and Herter 1990, Byrd and Day 1986). I recorded birds with a Sony TCD-D10PROII Digital Audio Tape recorder (sampling rates 32, 44.1, and 44.2 kHz) or Fostex FR-2 solid-state recorder (sampling rate 48.1 kHz), with Senheiser MKH 70 or MKH 816 directional microphones. My recording sessions totaled ~80 hrs. Recordings were analyzed with Raven 1.2.1 (Bioacoustics Program, Cornell Lab of Ornithology, New York). I referred to the briefest sound elements in spectrograms as units and classified them to several types (note types). Acoustic measurements included duration, frequency, modulation of the carrier frequency, and harmonic structure (F, Frequency; F_n, frequency of n^{th} harmonic; F_0, fundamental frequency; F_μ, Frequency of the harmonic that has the highest intensity in the power spectrum; CFn, carrier frequency of n^{th} harmonic; FM, frequency modulation; Chapter Three).

Following Miller (1996), McCracken and Sheldon (1997), Burns (1998) and Price and Lanyon (2002), I identified 28 probable homologies from above total repertoires. Continuous characters were assigned to discrete categories (character states 0,1 and 2) by the method of Price and Lanyon (2002). For each continuous character, 95% confidence

intervals were determined from three representative individuals, and the non-overlapping regions of character distribution were considered as a character state. Continuous characters that could not be subdivided by this method were excluded from the analysis. Other characters were characterized as "present" or "absent" (Price and Lanyon 2002). The exceptions were F_{μ}, song structure, FM of CF in songs and sequentially graded elements. Character states that represent Cassin's Auklet were assigned the '0' state except when it represented the middle state of three non-overlapping states ('1').

5.3.2. Selection and scoring of syringeal characters

Following Cannell (1988), the vocal tract (from bronchi to approximately mid trachea) were removed from fresh specimens of all *Aethia* species from Buldir Island, and stored in 70% ethanol. Specimens of Cassin's and some of the Parakeet Auklet specimens were taken from the collection of E.H.Miller. Three specimens (including both sexes) from each species were examined. I measured the preserved syrinx and syringeal muscles under a dissecting microscope with an ocular micrometer (calibrated with a stage micrometer), with 10-power magnification. Measurements were taken to ± 0.1 mm on the following variables: 1) dorsoventral depth of the syrinx, on left and right sides (mean was used in analyses); 2) breadth of the syrinx, from dorsal aspect; and 3) maximal diameter of *M. tracheolateralis* and *M. sternotrachealis* on left and right sides (mean was used in analyses). After measurement, vocal tracts were stained for cartilage and calcium phosphates with alcian blue and alizarin red, and then stored in 90% glycerin (Cannell 1988). With the same microscope setup, I estimated the degree of calcification in

syringeal rings, bronchial semirings, and pessulus, and the amount of ring fusion in calcified rings. Correlation of syringeal size with body size (PC1 on syringeal variables with body mass) was computed with JMP 7.0 (2007. SAS Institute inc.). Data for mean body mass were taken from Jones (1993a, b) and Gaston and Jones (1998).

5.3.3. Molecular Phylogeny

Based on a combined data set of 7496bp from four mtDNA loci (12S [549 bp], 16S [1009 bp], COI [1080 bp], ND2 [948 bp], and CytB [1045 bp]), and a nuclear locus, Recombination Activating Protein (Rag-1; 2727 b), Perreira & Baker (2008) consistently identified auklets as a monophyletic group, with *Ptychoramphus* as the sister to *Aethia*. However they were unable to resolve relationships within *Aethia*. I recompiled the data for Aethiini used by Pereira and Baker (2008) and those for the 12S locus in Moum et al. (1994) from the National Center for Biotechnology Information (NCBI; GenBank). Maximum likelihood analyses for the molecular characters were performed with PAUP 4.10b, with the exhaustive search option, and 10,000 bootstrap replicates (Swofford 2002).

5.3.4. Reconstruction of character changes

The most parsimonious vocal and syringeal phylograms were estimated by PAUP, with the exhaustive search option. All 38 characters were assigned equal weight. I mapped acoustic and syringeal characters onto my molecular phylogeny with PAUP (with MulTrees option). The consistency index (CI: Kluge & Farris 1969) and retention index

(RI: Farris 1989) of each character were used to evaluate overall congruence between the molecular tree and the acoustic and syringeal phylogenies (Burns 1998, Omland and Lanyon 2000, Price and Lanyon 2002). Simple parsimony with either accelerated (ACCTRAN) or delayed (DELTRAN) character transformation was used to map and compare putative apomorphies (Maddison and Maddison 1992). MacClade 3.5 (Maddison and Maddison 1992) was used to map character states onto the molecular phylogeny, and to estimate character changes based on the molecular topology. I used a two-tailed Wilcoxon signed-rank test to compare contrasts in CI values among phylogenetic trees (SPSS release 15.0, SPSS Inc. 2006, Chicago, IL).

5.4. RESULTS

Vocal repertoire of auklets is complex and large (22 total display types), and is characterized by 1-5 frequency modulated and harmonically rich note types (28 notes across species) arranged sequentially in varied combinations (Chapter Three). Characteristics of notes and appearance of them in displays were intraspecifically consistent. Two groups were identified based on syntactical arrangement of notes: (1) alternate arrangement of note types in Cassin's and Parakeet Auklets; and (2) arrangement of sequentially graded note types through the display, in Whiskered and Least Auklets. The repertoire of Crested Auklet was closest to that of Whiskered Auklet, however some display types showed alternate arrangement of elements as in the other vocal group (Chapter Three).

5.4.1. Syringeal anatomy

Syringeal morphology was similar across auklet species, and resembled that of other alcids (Warner 1968, Miller et al. 2008). Tracheal rings were cartilaginous and separated from elastic membrane. Rings were notched in dorsal and ventral median lines. The syrinx of the Crested Auklet was the largest, followed by Cassin's, Parakeet, Whiskered and Least Auklets (Table 5.1). Syringeal size (as reflected in PC1 on syringeal variables) was positively correlated with body mass ($F_{1,12} = 13.63$, $p = 0.003$, $R^2 = 0.53$). However, size of syringeal musculature varied little across species, and was not concordant with syringeal dimensions (Table 5.1). Calcification of the tracheal ring was limited to the posterior portion of the trachea. The greatest degree of calcification (~7 calcified rings) occurred in the Cassin's Auklet; *Aethia* auklets had ~5 calcified rings (Table 5.1).

5.4.2. Acoustic and syringeal character matrix

Table 5.2 summarizes the 38 acoustic and syringeal characters. Characters 1-10 and 18-20 represented the structural information of acoustics, and complexity of the syrinx . Characters 11-28 represented temporal variation, and 29-38 described syringeal anatomy. Characters 1,5,7,11,14,16-38, each have two alternative character states (0,1), and the remainder each have three non-overlapping states (0-2; Table 5.2). I coded behavioral characters (25-28) as "present" or 'absent' to avoid subtle intraspecific variability. Of the 38 characters used, 19 were parsimony-informative (Table 5.3). The shortest tree obtained from simple parsimony required 56 character changes (Table 5.3, Figure 5.1). In the rooted tree, Cassin's Auklet was basal to *Aethia* , Parakeet Auklet was basal to the

remaining auklets, and Crested and Whiskered Auklets were sister groups (Figure 5.1). The length of the remaining 14 trees varied from 57 to 66 steps.

5.4.3. Molecular phylogeny

When the loci used in Pereira and Baker (2008) were considered separately, 12S gave very strong support for Whiskered Auklet and Least Auklet as sister species, whereas COI, ND2, and Rag-1 gave moderate to weak support for Least Auklet as the outgroup to the other *Aethia*, and Cytb paired Least Auklet with Parakeet Auklet with moderate support. The 16S locus did not provide bootstrap support for any particular arrangement. I repeated the phylogenetic analysis of 7347bp from all five loci, with the 12S data from Moum et al. (1994) in place of that from Perreira & Baker (2008). A Maximum Likelihood Analysis (6-ST model with 10,000 bootstrap replicates) with Cassin's Auklet (*Ptychoramphus*) specified as the outgroup, places Least Auklet outside the other three Aethia spp., with bootstrap support of 71% (Figure 5.2). The separation of Parakeet, Crested, and Whisked Auklets remains an unresolved tritomy.

Table 5.1

Summary of descriptive statistics on syringeal characters of auklets (Aethiini). The numbers in the header row indicate the variable numbers in the Table 5.2.

Auklet sp.	Dimensions (±SD; mm)				No. of calcified rings (range)					
	29	30	31	32	33	34	35	36	37	38
Cassin's	4.9(0.7)	4.6(0.3)	0.8(0.0)	1.2(0.1)	7(6-7)	3(0-3)	5(4-5)	7(6-7)	7(3-7)	partial
Crested	5.1(0.1)	5.5(0.1)	0.9(0.0)	2.2(0.0)	5(4-5)	0(0)	0(0)	5(4-5)	0(0)	partial
Least	3.8(0.1)	4.1(0.2)	0.9(0.0)	1.5(0.0)	5(4-5)	2(2)	3(3)	4(4)	4(2-4)	complete
Parakeet	4.4(0.3)	4.7(0.3)	0.9(0.1)	1.5(0.2)	5(4-5)	2(0-2)	4(3-4)	4(4)	4(0-4)	complete
Whiskered	3.9(0.3)	4.0(0.2)	0.9(0.0)	1.4(0.3)	5(4-5)	1(0-1)	5(3-5)	5(3-5)	3(0-3)	partial

Table 5.2

Summary of acoustic and syringeal characters and character states used in the phylogenetic comparison.

Vocal characters

1. Number of note types in the repertoire. 0: ≤ 5, 1: >5.
2. Minimum note type length. 0: < 20ms, 1: 20-30 ms, 2: > 40 ms.
3. Maximum note length. 0: < 500 ms, 1: 500 - 1500 ms, 2: >1500 ms.
4. Minimum F_{μ} 0: <1.0 kHz, 1: 1.0-1.5 kHz, 2: > 1.5 kHz.
5. Maximum F_{μ}. 0: < 2.5 kHz, 1: 2.5-4.0 kHz, 2: > 4.0 kHz.
6. Most expressed harmonic. 0: F_0; 1: F_1, F_2 or F_3; 2: variable.
7. Minimal F_0. 0: > 1.5 kHz, 1: < 1.5 kHz.
8. Greatest number of frequency peaks in a note. 0: < 20, 1: 20-40, 2: > 40.
9. Minimal FM in a note. 0: < 0.6 kHz, 1: > 0.6 kHz.
10. Maximal FM in a note. 0: < 1.5 kHz, 1: 1.50-2.25 kHz, 2: > 2.25 kHz.
11. Number of vocalization types in repertoire. 0: ≤ 4, 1: > 4.
12. Maximal length of vocalization. 0: > 22 s, 1: < 22 s.
13. Minimal length of vocalization. 0: > 2.2s, 1: < 2.5s.
14. Maximal number of note types in a vocalization. 0: < 5, 1: > 5.
15. Minimal note spacing in a vocalization. 0: > 10 ms, 1: < 10 ms.
16. Level of structural organization in vocalization. 0: Lengthy, continuous, poorly defined; 1: brief and differentiated into introduction, body, end.
17. Presence of pulses (brief note types) in vocalization. 0: present, 1: absent.

18. Presence of pure tones. 0: absent, 1:present.

19. Presence of trills (note types with very rapid FM). 0: absent, 1: present.

20. Presence of broadband noise. 0: present, 1: absent.

21. Presence of FM along CF in the display. 0: high, 1: low.

22. Alternate and repeated arrangement of several note types in vocalization. 0: present, 1: absent.

23. Sequentially graded note type arrangement in vocalization. 0: present, 1: predominant.

24. Clustered arrangement of notes in vocalization. 0: present, 1: absent.

25. Formation of rafts and associated vocalization at sea. 0: absent, 1: present.

26. Aerial vocalization. 0: present, 1: absent.

27. Synchronous vocalization by several birds at the colony. 0: predominant, 1: rare.

28. Duet (display delivered by two individuals where each participant contributes to a specific section). 0: present, 1: absent.

Syringeal characters

29. Syringeal width. 0: < 4.4 mm, 1: ≥ 4.4 mm.

30. Mean syringeal depth. 0: ≤ 4.8 mm, 1: ≥ 4.8 mm.

31. Mean width of *M. tracheolateralis*. 0: ≤ 0.9 mm, 1: ≥ 0.9 mm.

32. Mean width of *M. sternotrachealis*. 0: ≤ 1.6 mm, 1: ≥ 1.6 mm.

33. Number of calcified tracheal rings, 0: ≥ 5 rings, 1: ≤ 5 rings.

34. Completely calcified tracheal rings. 0: present, 1: absent.

35. Ventral syringeal calcification. 0: present, 1: absent.

36. Dorsal syringeal calcification. 0: ≥ 5 rings, 1: ≤ 5 rings.

37. Fused calcified rings. 0: present, 1: absent.

38. Calcification of pessulus. 0: complete, 1: partial.

Table 5.3

Character matrix for acoustic and syringeal phylogram. Character numbers and states as in Table 5.2; abbreviations for species are; CaAu, Cassin's Auklet (*P. aleuticus*); CrAu, Crested Auklet (*A. cristatella*); LeAu, Least Auklet (*A. pusilla*); PaAu, Parakeet Auklet (*A. psittacula*); WhAu, Whiskered Auklet (*A. pygmaea*).

Character state																																					
										1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
CaAu	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CrAu	0	2	1	0	0	2	1	0	0	0	1	1	1	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1
LeAu	0	0	0	2	2	2	0	1	1	2	0	1	1	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
PaAu	0	1	2	0	1	0	1	2	0	2	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0
WhAu	1	1	1	2	2	1	1	0	0	1	1	1	1	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	1

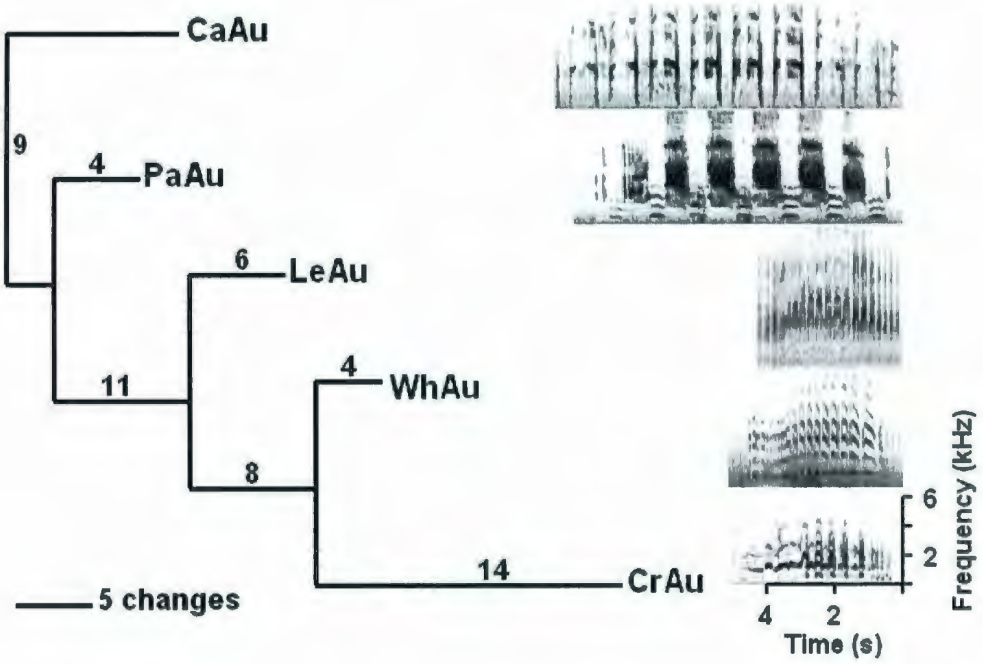

Figure 5.1

Minimum length tree for the vocal and syringeal character matrix generated by simple parsimony. Numbers on each branch indicate number of character changes. A representative display type of each species is also shown (Cassin's Auklet, Kut-I-er; Parakeet Auklet, Whinney; Least Auklet, Chatter; Whiskered Auklet, Staccato Beedoo; Crested Auklet, Trumpet). Abbreviations for the species are as in Table 5.3.

5.4.4. Reconstruction of change in vocal and syringeal characters

Disagreement between the vocal characters and molecular phylogeny, was evident from the low CI and RI values (Table 5.4). The overall CI and RI were 0.70 and 0.10 respectively, where temporal and syringeal characters had a greater CI (0.75 and 0.71 respectively). However, frequency-related characters showed a lower CI (0.65; Table 5.4). The Pereira and Baker (2008) phylogeny, which was based on relatively low bootstrap support, indicated a greater overall congruence (CI 0.76, RI 0.33), however, CI values of the two molecular trees were not significantly different (Wilcoxon signed-rank test; $p = 0.157, 0.655, 0.083$ for temporal, frequency and syringeal characters respectively). Based on the molecular tree proposed in this study, only 38% of temporal and syringeal characters had low CI values compared to 66% of that of frequency related characters (Table 5.5). The smaller number of vocal and syringeal character changes in the branches among nodes (Figure 5.3) reflected the poor fit between vocal and molecular trees. However, in the tree proposed by Pereira and Baker (2008), about 30% of the changes were concentrated at the branch leading to the Least Auklet. In the absence of the Least Auklet, acoustic traits mapped perfectly on the tree (CI 0.98, RI 0.91).

Table 5.4

Summary of character analysis for the different vocal and syringeal attributes.

	Number of characters	**CI**	**RI**
Total	38	0.70	0.10
Vocal characters	28	0.70	0.12
Temporal	16	0.75	0.00
Frequency	12	0.65	0.18
Syringeal characters	10	0.71	0.00
Tree without Parakeet Auklet	38 (4 taxa)	0.86	0.50

Table 5.5

Measures of homoplasy for vocal and syringeal characters mapped on to the molecular phylogeny.

Character		CI	Character		CI
	Temporal characters				
1	Number of note types	1.0	**7**	F_0	0.5
2	Minimal note length	1.0	**8**	Greatest number of peaks in a note	0.7
3	Maximal note length	1.0	**9**	Lowest range FM	1.0
11	Number of vocalization types	0.5	**10**	Highest range FM	0.7
13	Minimal length of vocalization	1.0	**18**	Pure tones	1.0
12	Maximal length of vocalization	1.0	**19**	Trills	0.5
14	Number of note types in a vocalization	1.0	**20**	Broadband noise	0.5
15	Minimal note spacing	0.5	**21**	FM in vocalization	1.0
16	Structural organization of vocalization	0.5	**23**	Sequentially graded note types	0.5
17	Pulse	1.0			
22	Alternate arrangement of note types	0.5		**Syringeal characters**	
24	Clustered arrangement of note types	0.5	**29**	Syringeal width	0.5
25	Formation of rafts	1.0	**30**	Mean syringeal depth	1.0
26	Aerial vocalization	1.0	**31**	Mean width of M. tracheolateralis	1.0
27	Synchronous vocalization	1.0	**32**	Mean width of M. sternotrachealis	1.0
28	Duet	0.5	**33**	Number of calcified rings	1.0
			34	Completely calcified rings	0.5
	Frequency characters		**35**	Ventral syringeal calcification	1.0
4	Minimal F_μ	0.7	**36**	Dorsal syringeal calcification	1.0
5	Maximal F_μ	0.7	**37**	Fused syringeal rings	0.5
6	Harmonic level of F_μ	0.5	**38**	Calcification of pessulus	0.5

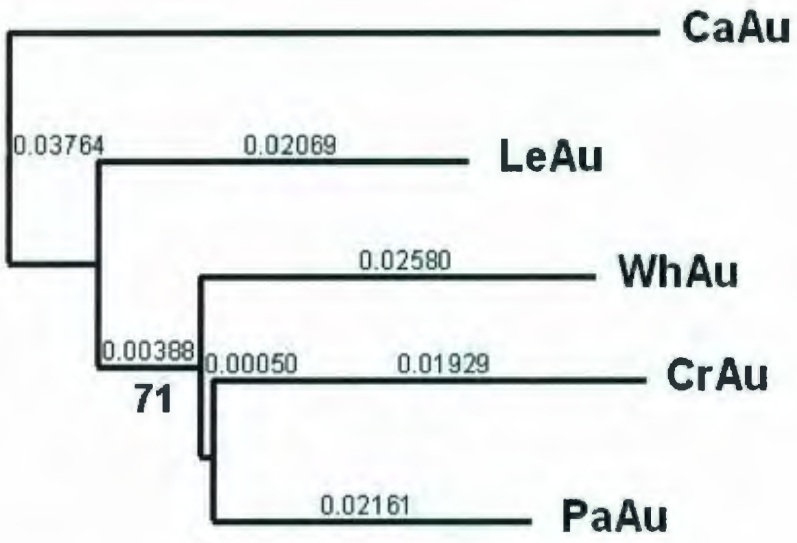

Figure 5.2

Molecular phylogenetic relationship of auklets based on a combination of mitochondrial and nuclear DNA characters; 12S, 16S, COI, ND2, CytB and RAG-1. The numbers on the branches represent maximum likelihood distances for each branch; bold number (71) indicates the bootstrap support for 10,000 replicates. Abbreviations for the species are as in Table 5.3.

5.5. DISCUSSION

The Aethinii auklets have undergone a spectacular adaptive radiation within the Alcidae (Jones 1999), with striking diversification of visual displays, yet the pattern of vocal display diversity remains enigmatic. I have sought to elucidate some basic evolutionary forces that determine vocal display diversity in these seabirds. I compared vocal displays of each auklet species in relation to molecular phylogeny, an approach that has been proven effective in elucidating evolutionary patterns (e.g., Burns 1998, Slabbekoorn et al. 1999, Price and Lanyon 2002, Päckert et al. 2003, Kort and ten Cate 2004), although weaknesses have been outlined by Atz (1970), Frumhoff and Reeve (1994), Westoby et al. (1995), Omland and Lanyon (2000), and Masters (2007).

I obtained poor concordance between acoustic and syringeal traits and the molecular phylogeny of Aethiini (CI, 0.70 and RI 0.10; Table 5.4). The disparity is most pronounced in frequency-related vocal characters and syringeal characters (CI 0.65 and 0.71 respectively; Table 5.4). Temporal characters reflect greater congruence (CI 0.75). Overall, 17 vocal and syringeal characters (45%) showed evidence of character reversal or convergence that include seven frequency related characters, six temporal characters, and four syringeal characters; support the notion that temporal and syringeal characters reflected phylogenetic patterns more closely than frequency-related vocal characters (McCracken and Sheldon 1998). The position of the Parakeet Auklet was the most discordant among trees (Table 5.4, Figure 5.3): when this species was removed from the analysis, the trees matched reasonably well (Table 5.4).

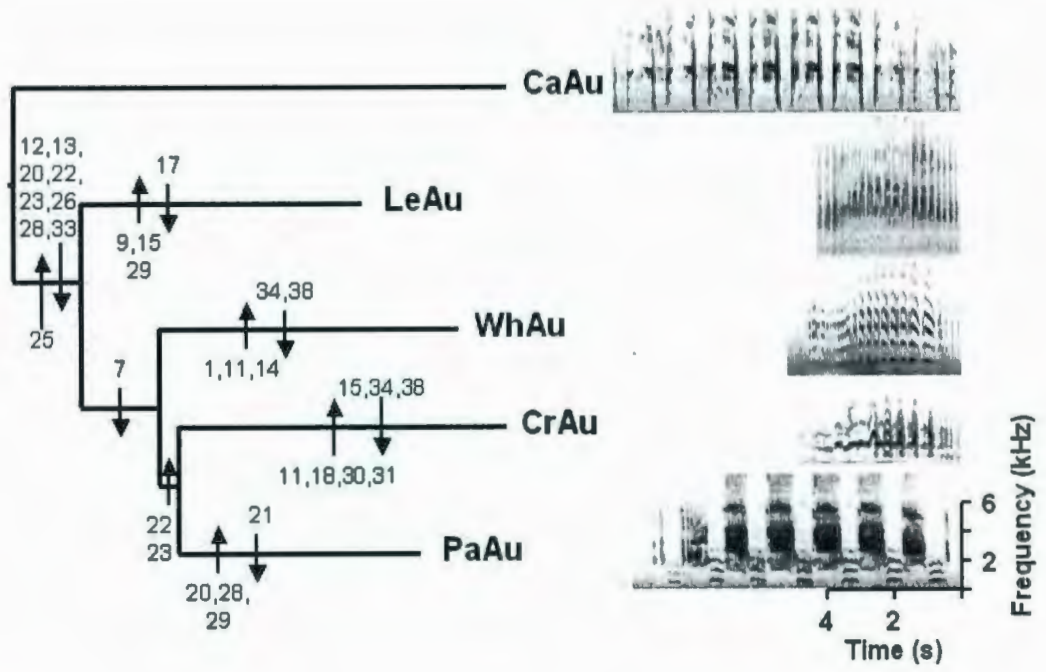

Figure 5.3

Evolutionary changes of vocal and syringeal characters reconstructed on the molecular phylogeny shown in Figure 5.2. Unambiguous character changes are shown as arrows along the branches (up arrows for gain/increase and down arrows for loss/decrease for particular vocal or syringeal character) with the character numbers as in Table 5.2. Spectrograms of advertisement display (as in Figure 5.2) are also aligned to visualize some of the changes that took place along the phylogeny. Abbreviations for the species are as in Table 5.3.

The CI depends on the number of characters used in the analysis, and it tends to decline with an increasing number of characters (Wimberger and Queiroz 1996). Because my analysis encompassed a large number of characters, CI might have been expected to be smaller. However, the lower RI value, which does not correlate with the number of characters used (Price and Lanyon 2002), also reflected lower congruence.

The similarity of vocalization in Cassin's and Parakeet Auklet species pair contradicted most strongly with the molecular tree (Figures 5.1-5.3). Element (note types) arrangement and some of the display types of these two species were similar. For example, Cassin's Auklet's Kree-er and Kut-I-er displays are acoustically similar to Parakeet Auklet's Raft-whinny and Whinny, respectively. They were, however delivered under different conditions; Kut-I-er and Kree-er are delivered in front of the burrow and as an aerial display, whereas Whinney and Raft-whinney are delivered mainly at the sea (Chapter Three). Vocal homologies were evident in the repertoire of Crested and Whiskered Auklets, which was mainly characterized by sequential gradation of element complexity. Crested Auklet's Trumpet, Cackle and Bark were structurally and functionally analogous to the Whiskered Auklet's Staccato-beedoo, Duet-beedoo and Bark respectively (Chapter Three). Furthermore, the Least Auklet repertoire consisted of highly graded note types with rapid, frequency-modulated trills, which was closest to the repertoires of the Whiskered Auklet (Chapter Three).

The importance of habitat for vocal diversification has been previously suggested (Morton 1975, Marten and Marler 1977, Blumenrath and Dabelsteen 2004, Nicholls and Goldizen 2006). Since vocal displays are used for communication, natural selection

favors signals with optimum signal transmission (Endler 1992, Bradbury and Vehrencamp 1998). Hence, habitat characteristics such as vegetation cover, density, and the amount of reverberation from rocks, sound-absorptive loose soil, etc., can alter both frequency (Wiley 1991, Badyaev and Leaf 1997, Bertelli and Tubaro 2002) and temporal attributes of the signal (Wiley 1991, Dabelsteen et al. 1993, Nicholls and Goldizen 2006). Frequency attributes are more affected by ecological forces (McCracken and Sheldon 1997, also see Nicholls and Goldizen 2006). This could partly explain the greatest similarity observed between the repertoires of Cassin's and Parakeet Auklets (Figure 5.4A). Both Parakeet and Cassin's auklets had higher F_{μ}, which may have been selected for close-to-ground vocal display (Marten and Marler 1977, Marten et al. 1977) as both these species breed in grassy slopes with soft soil, and vocalize from and in front of the burrows (Thoresen 1964, Manuwal and Thoresen 1993, Jones et al. 2001, Chapter Three). Each display is associated with specific location and situation in auklets (Chapter Three), hence the selection pressure enforced by habitat on different display types could be variable. The use of nearly complete repertoires sheds light on selection pressures acting on different display types within a species' repertoire.

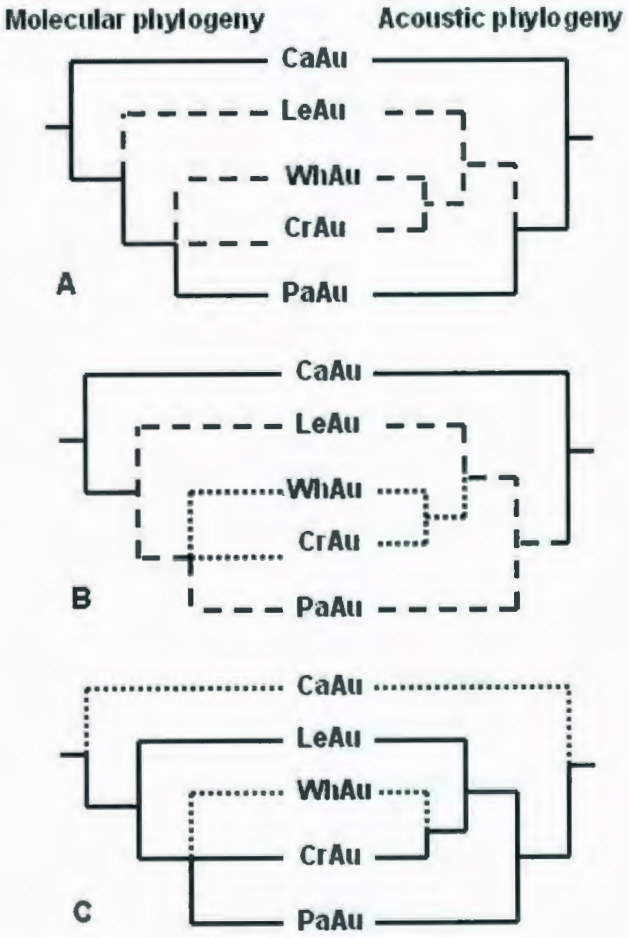

Figure 5.4

Some likely explanations for vocal divergence in Aethiini. A) The effect of breeding substrate; vegetated soft soil (solid line) and rock crevices (broken line), B) the effect of ornament expression; highly ornamented (dotted line), ornamented (broken line) and sparsely ornamented (solid line), C) colony attendance behavior; nocturnal (dotted line) and diurnal (solid line).

Even though the knowledge of sexual differences in auklet vocalization is sparse, some displays differ between sexes that hint a possible role of sexual selection acting on these traits. The Kut-I-eer of the Cassin's Auklet (Manuwal and Thoresen 1993), Trumpet and Cackle of the Crested Auklet (Jones 1993a, 1998), Least Auklet Chatter (Jones 1993b), Parakeet Auklet Raft-whinny and Whinny (Jones et al. 2001), and Staccato-beedoo and Duet-beedoo of the Whiskered Auklet all function as exclusive or nearly exclusive male courtship displays (Chapter Three). Similarly, advertisement displays can be subjected to sexual selection (Catchpole 1982), and such displays are prevalent in auklet vocal repertoire. Sexually-selected displays can evolve rapidly (Kaneshiro 1988, Uy and Borgia 2000), hence homoplasy would be common when the options for change are limited in such divergence (Atz 1970, Omland and Lanyon 2000, Masters 2007). This may partly explain the lower congruence between acoustic and syringeal traits with molecular phylogeny.

Facial ornament differences are congruent with recent phylogenetic models in Aethiini (Figure 5.2; this study and Pereira and Baker 2008): Cassin's Auklet, with the least ornamentation, is the outgroup to the more ornate species, and the similar patterns of Crested and Whiskered auklet are the most recently evolved. Forward-curving crest and elongated facial feathers, dark throat, belly, and the citrus feather odor (Hagelin et al. 2003, Jones et al. 2004a, Douglas et al. 2004) are shared by these most recent *Aethia* species (Jones 1999). The appearance of Least and Parakeet Auklets is similar: pale belly and throat, similar body proportions, and the absence of the crest, which is not

reflected in my molecular tree, however (Figure 5.2). Vocalizations also have followed the same overall pattern of visual and chemical displays (Figure 5.4B). However I did not notice a reduction or gain in complexity along the tree. Visual ornaments can play a role in species divergence (Kaneshiro 1988, Omland and Lanyon 2000, Burns 1998, Coyne and Orr 2004), and in Aethiini, speciation appears to have been associated with the selection on display traits (Jones 1999). Similar sexual selection (that acted on the visual traits) could have acted on vocal traits and led to the observed parallel patterns of vocal diversification (Figure 5.4B).

Auklets' variable colony attendance behavior might be related to other ecological factors such as predation, day length, and nest site competition (Byrd and Williams 1993, Gaston and Jones 1998, Hunter et al. 2002). To reduce predation risk, alcids either tend to form large colonies or become nocturnal and distribute more sparsely (Jones 1993a, b, Zubakin and Konyukhov 1999, Hunter et al. 2002). However, nocturnal colony attendance behavior is not linked in anyway with their activity patterns, as they forage and socialize during daytime at sea (Gaston and Jones 1998). Nocturnality can affect vocal divergence (Park et al. 1940, Jones et al. 1989a), and some nocturnal alcids show greater complexity in their vocal repertoires (Jones et al. 1987, 1989a, b, Drost and Lewis 1995, Nelson 1997). However, the complexity of repertoires of the two nocturnal auklets is not very different from their diurnal congeners (Figure 5.4C; this study and Chapter Three).

Patterns of divergence in Aethiini vocal behaviour are likely result from genetic relatedness, and ecological and social selection. Since all other proposed phylogenies

agreed on the placement of Cassin's Auklet as basal to *Aethia*, I might have expected to see a similar divergence in Cassin's Auklet's vocalization. However, vocalizations of this species were most similar to that of a much younger *Aethia* spp. (Parakeet Auklet). Although some relationships are congruent among the compared phylogenies, my results did not fully support the hypothesis that the phylogenetic relationships play the greatest role in vocal diversification. Instead, together with the phylogenetic relatedness, a combination of social and ecological factors, such as breeding habitat and other social displays seem to be the dominant driving force. My work underlines the possibility that display-related traits can rapidly diverge in patterns at odds with phylogenetic relationships. I suggest that both vocal and visual displays may have been evolved in tandem and contributed to species divergence in auklets. Marine habitat can affect on signal design (Wiley and Richards 1982) and all auklets except Cassin's Auklet perform vocal displays in groups (rafts) at sea near their colonies. Future studies should look into the vocal behavior at sea to determine the effects of marine environment on the vocalization, and specific role of other signals (e.g. visual display) on vocal divergence in Aethiini.

5.6. ACKNOWLEDGEMENTS

I thank J. C. Williams and G. V. Byrd for logistic support and permission to conduct research in the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge, G. Humphries and C. Small for the assistance in the field, and A. J. Baker and H. D. Marshall for the comments on the molecular data and analysis. I am especially grateful

for the Macaulay Library of the Cornell Lab of Ornithology for providing some of the recording equipment and technical assistance. I acknowledge the support provided by the captain and crew of the vessel M/V Tiglax for transportation to the Egg and Buldir Islands. Natural Sciences and Engineering Research Council (NSERC) Canada - Discovery Grant held by I. L. Jones provided the major funding for this study. Support for the phylogenetic analyses was provided by a Grants and Contracts agreement from the Canadian Department of Fisheries and Oceans (DFO) to S. M. Carr.

CHAPTER SIX

SUMMARY

Elaborate visual and acoustic traits received considerable attention in many early writings in behavioural and evolutionary ecology (Darwin and Wallace 1858, Darwin 1859, 1871, Wallace 1878, Huxley 1931, Mayr 1940, Fisher 1958, Tinbergen 1959, Lorenz 1970, 1971). These provided the foundation for research in recent decades focused on more detailed explanations for the expression of such traits (e.g., Andersson 1994, Purvis and Rambaut 1995, Martins 1996, Amundsen 2000, Slabbekoorn and Smith 2002, Marler and Slabbekoorn 2004). In this dissertation I explored several poorly discussed aspects of the ecology of ornamental trait expression in a remarkable group of North Pacific seabirds.

My work presents the first evidence for a possibly widespread but overlooked mechanosensory function of elongated feathers in birds. A tactile function for elongated plumes may explain the origin and maintenance of such feather adornments in various groups of birds. This dissertation further provides the most detailed acoustic analysis for any group within the Alcidae, and provides an essential baseline vocal ethogram for future research on the family. Overall, this thesis assessed some of the phylogenetic, social and environmental factors that were hypothesized to contribute to the evolution of visual and acoustic traits in auklets (Aethiini).

6.1. MAIN POINTS

The elaborate facial plumes of the Whiskered Auklet function as a mechanosensory device to aid navigation in the absence of visual clues in breeding crevices. This species'

white antenna-like ornamental plumes are derivatives of filoplumes that are the known feather type for tactile use (Küster 1905, Stettenheim 1972). The Whiskered Auklet's crest feathers are modified contour feathers. To my knowledge, this study provides some of the first direct evidence for the sensory function of contour feathers (Brown and Fedde 1993). Birds with longer crest and facial plumes showed greater dependence on those traits inside the test chamber, suggesting a possible relationship of feather length and its user's dependence on the trait. My results hopefully will provide the stimulus for future research on sensory use of ornamental feathers that hitherto have been assumed to function exclusively for signalling.

Environment likely played a role in the evolution of tactile function. The crest ornament and mechanosensory use are confined to peripheral branches of the genus *Aethia* that nest in deep-crevices. A survey across non-passerine bird families provided further comparative evidence that this sensory function might also occur in the wild as an adaptation to negotiate complex habitats or low light conditions. The expression of elongated facial plumes is rare but widespread in non-passerine birds (33 of 102 families express long facial plumes). The positive correlation between the expression of long facial plumes and habitat complexity suggested that these traits are more likely to evolve in species that live in complex habitats or are active in low light conditions. I was unable to pinpoint the origin or maintenance of this tactile use. However, once protruding feathers evolved, either sexual selection through mate choice (Jones 1990, Jones and Hunter 1993, 1999, Andersson 1994) or natural selection for camouflage (Strijbos 1927,

Perrone 1981, Lorek 1992, Baker and Parker 1979, Galeotti and Rubolini 2007) could explain further elaboration.

The Aethinii auklets demonstrate a striking diversification of visual displays (Gaston and Jones 1998, Jones 1999), yet the patterns of vocal display diversity remain enigmatic. I looked at both acoustic and visual traits as display types that have been shaped by social selection (Andersson 1994, Gaston and Jones 1998). Vocal repertoires of breeding adult auklets are complex and large (~25 call types across species). Two main patterns of acoustic organization were identified: alternating or sequentially graded arrangement of notes within display. Cassin's and Parakeet Auklets are very similar vocally, but are not normally grouped together. Whiskered and Crested Auklets are vocally similar, and appear to be sister species on molecular evidence (Pereira and Baker 2008, Chapter Five). A phylogenetic analysis using vocal and syringeal characters in relation to a fairly well resolved molecular phylogeny revealed that some relationships are congruent with the phylogeny. However, the results did not fully support the hypothesis that phylogenetic relationships play the greatest role in vocal diversification. Overall, auklet vocalizations may have been subjected to both natural and social selection that caused different species to diverge in ways radically at odds with their phylogenetic relationships.

6.2. METHODS DEVELOPED

I developed an experimental chamber to study exploratory behaviour of nocturnal and crevice-dwelling diurnal birds. Light-tight chambers with the dimensions of the nesting

crevice were designed and constructed, and a digital camcorder with built in infrared light source recorded the subjects' behavior in the absence of visible light. The wavelength of infrared light sources commonly available in camcorders with '0 lux recording capability' (peak wavelength ~850 nm) is above the peak spectral sensitivity of birds (between 350-600 nm; Liebman 1972, Bowmaker and Martin 1985, Bowmaker et al. 1997, Hart 2001), an opportunity for field ecologists to explore. The camera-based visual scoring setup was useful in situations where the test subjects do not produce sufficient mechanical force to consistently measure the behavioural response using a remote detection system (e.g., use of remote touch or pressure detectors). The setup was portable, commercially inexpensive to produce, and withstood severe weather conditions that helped to conduct experiments in the field; hence it increased sample size and decreased overall stress for test subjects.

The effects of opposing selection pressures can be minimized using manipulative experiments (Schluter et al. 1991). I used the closely related, crestless, Least Auklet as a natural control, to which an artificial crest was attached. Attachment of artificial novel traits on live animal models is a rare practice in behavioural ecology (some examples for similar alterations: Grether and Grey 1996, Witte and Curio 1999, Plenge et al. 2000, Rowe et al. 2001). Similar frequency of head bumps in the presence and absence of the artificial crest supported my study design; the reduction of head bumps in Whisked and Crested Auklets was not a simple physical barrier effect of the forward-projecting crest plumes.

Single call types are used most often in phylogenetic analysis and in contrast vocal repertoires rarely used. Analysis of multiple sound classes is potentially more informative in groups with complex and large repertoires such as auklets (Price and Lanyon 2002, Isler et al. 2007). However, the greater effect of variable selection forces that mask specific evolutionary patterns is the major drawback of this method, as exemplified by my work with auklets.

The phylogenetic comparative method has often been used to infer evolutionary mechanisms (Wenzel 1992, Martins 1996, Burns 1998, Slabbekoorn et al. 1999, Martins 2000, Price and Lanyon 2002, Päckert et al. 2003, Kort and ten Cate 2004). Two commonly used methods were employed in this study (Gittleman and Luh 1992, Martins 1996). With the use of vocal and syringeal characters plus a molecular phylogeny, I investigated factors leading to vocal divergence. Furthermore, a pairwise comparison that consists of all non-passerine bird families was used to examine statistical correlations between the long facial feathers and habitat complexity.

6.3. RECOMMENDATIONS AND FUTURE DIRECTIONS

I established a new explanation for elongation of facial feathers, mechanosensory function. Similar traits, such as streamers on pin- and forked-tails, projecting feathers on wings and body, that are routinely inferred to function primarily as visual signals during courtship (Darwin 1871; Kirkpatrick and Ryan 1991; Andersson 1994; Amundsen 2000) are all possible candidates for past and present mechanosensory use. Future studies need to investigate extensive nerve innervation or aggregation of mechanoreceptors on or near

these specialized feather ornaments to reveal the neuroanatomical and neurophysiological basis for the observed tactile use. A detailed phylogenetic study could elucidate the evolution of these tactile traits. The use of complex habitats is widespread; hence such a phylogenetic correlation requires a phylogenetic tree including all species that live in complex habitats to avoid overrepresentation of ornamented forms (Höglund 1989, Höglund and Sillén-Tullberg 1994), which I have not attempted here.

The lack of robust phylogenetic tree for Aethiini impeded the ability to resolve acoustic relatedness of auklets. The development of refined molecular techniques or inclusion of greater number of gene loci for analyses holds the promise for a fully resolved tree for this long unresolved clade (Pereira and Baker 2008). With the aid of such trees the relative placement of the Parakeet Auklet in *Aethia* and the underlining reasons for its close vocal affinity with the Cassin's Auklet will be resolved.

6.4. CLOSING THOUGHTS

"...we can understand on the principles of inheritance, how it is that the thrush of South America lines its nest with mud, in the same peculiar manner as does our British thrush..." (Darwin 1859)

A comparative view into elaborate traits and behavioural patterns, as Darwin hinted in the above quote, could reveal the evolutionary pasts of ornaments and animal display. In this dissertation I looked at several of such elaborate traits and tried to understand how they diverge and relate to each other. Furthermore, I have discussed several evolutionary patterns that ecologists can learn from observing the living world. Forces of natural and sexual selection are neither mutually exclusive nor act on a single trait at a time. This dissertation emphasized the need for a broader experimental, comparative and phylogenetic approach, including multiple display types to elucidate the ecology of ornamental traits.

LITERATURE CITED

ALATALO RV, HÖGLUND J, AND LUNDBERG A. 1988. Patterns of variation in tail ornament size in birds. Biological Journal of the Linnean Society 34:363-374.

AMUNDSEN, T. 2000. Why are female birds ornamented? Trends in Ecology and Evolution 15:149-155.

ANDERSSON, M. 1982a. Female choice selects for extreme tail length in a widowbird. Nature 299:818-820.

ANDERSSON, M. 1982b. Sexual selection, natural selection and quality advertisement. Biological Journal of the Linnean Society 17:375-393.

ANDERSSON M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. Evolution 40:804-816.

ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ, USA.

ANDERSSON, M., AND Y. IWASA. 1996. Sexual selection. Trends in Ecology and Evolution 11:53-58.

ATHREYA, R. 2006. A new species of *Liocichla* (Aves: Timaliidae) from Eaglenest Wildlife Santuary, Arunachal Pradesh, India. Indian Birds 2:82-94.

ATZ, J. W. 1970. The application of the idea of homology to behavior. Pages 53-74 in Development and evolution of behavior (L. R. Aronson, E. Tobach, D. S. Lehrman and J. S. Rosenblatt, Eds.). Freeman, San Francisco, CA, USA.

BADYAEV, A. V. AND E. S. LEAF. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. Auk 114:40-46.

BAKER, R. R., AND G. A. PARKER. 1979. The evolution of bird colouration. Philosophical Transactions of the Royal Society of London B 287:63-130.

BAKER, A., S. PEREIRA, AND T. PATON. 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. Biology Letters 3:205-209.

BALMFORD, A., AND A. THOMAS. 1992. Swallowing ornamental asymmetry. Nature 359:487.

BAPTISTA, L. F. AND K. L. SCHUCHMANN. 1990. Song learning in the Anna Hummingbird (*Calypte anna*). Ethology 84:15-26.

BAPTISTA, L. F., AND P. W. TRAIL. 1992. The role of song in the evolution of passerine diversity. Systematic Biology 41:242-247.

BARROWCLOUGH, G. F., J. G. GROTH, AND L. A. MERTZ. 2006. The RAG-1 exon in the avian order Caprimulgiformes: phylogeny, heterozygosity, and base composition. Molecular Phylogenetics and Evolution 41:238-248.

BASOLO, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. Science 250:808-810.

BÉDARD, J. H. 1967. Ecological segregation among plankton-feeding alcidae (*Aethia* and *Cyclorrhynchus*). Ph.D. dissertation. University of British Columbia, Vancouver, BC, Canada.

BÉDARD, J. H. 1969. Adaptive radiation in Alcidae. Ibis 111:189-198.

BENZ, B. W., M. B. ROBBINS, AND A. T. PETERSON. 2006. Evolutionary history of woodpeckers and allies (Aves: Picidae): placing key taxa on the phylogenetic tree. Molecular Phylogenetics and Evolution 40:389-399.

BERTELLI, S. AND P. L. TUBARO. 2002. Body mass and habitat correlates of song structure in a primitive group of birds. Biological Journal of the Linnean Society 77:423-430.

BERTELLI, S., AND A. L. PORZECANSKI. 2004. Tinamou (Tinamidae) systematics: a preliminary combined analysis of morphology and molecules. Ornitologia Neotropical 15:293-299.

BERTELLI, S., N. P. GIANNINI, AND D. T. KSEPKA. 2006. Redescription and phylogenetic position of the early Miocene penguin *Paraptenodytes antarcticus* from Patagonia. American Museum Novitates, 3525.

BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London, UK.

BLUMENRATH, S. H., AND T. DABELSTEEN. 2004. Degradation of Great Tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. Behaviour 141:935-958.

BONCORAGLIO, G., AND N. SAINO. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology 21:134-142.

BORGIA, G. 1993. The cost of display in the non-resource-based mating system of the Satin Bowerbird. American Naturalist 141:729-743.

BOWMAKER, J. K., AND G. R. MARTIN. 1985. Visual pigments and oil droplets in the penguin, *Spheniscus humboldti*. Journal of Comparative Physiology A 156:71-77.

BOWMAKER, J. K., L. A. HEATH, S. E. WILKIE, AND D. M. HUNT. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. Vision Research 37:2183-2194.

BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principles of animal communication. Sinauer, Sunderland, MA, USA.

BRADSTREET, M. S. W. AND D. R. HERTER. 1991. Seabird colonies, marine birds and mammals of the Unimak Pass area: abundance, habitat use and vulnerability. US Fish and Wildlife Service, Alaska Regional Office, Anchorage, AK, USA.

BRENOWITZ, E. A. 1982. Long-range communication of species identity by song in the Red-winged Blackbird. Behavioral Ecology and Sociobiology 10:29-38.

BRETAGNOLLE, V. 1996. Acoustic communication in a group of nonpasserine birds, the petrels. Pages 160-178 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, NY, USA.

BRIGHAM, R. M., S. D. GRINDAL, M. C. FIRMAN, AND J. L. MORISSETTE. 1997. The influence of structural clutter on activity patterns of insectivorous bats. Canadian Journal of Zoology 75:131-136.

BRO-JØRGENSEN, J., R. A. JOHNSTONE, AND M. R. EVANS. 2007. Uninformative exaggeration of male sexual ornaments in barn swallows. Current Biology 17:850-855.

BROOKS, R., AND J. A. ENDLER. 2001. Female guppies agree to differ: phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. Evolution 55:1644-1655.

BROOKE, M. L., S. HANLEY, AND S. B. LAUGHLIN. 1999. The scaling of eye size with body mass in birds. Proceedings of the Royal Society B 266:405-412.

BROWN, D. M., AND C. A. TOFT. 1999. Molecular systematics and biogeography of the cockatoos (Psittaciformes: Cacatuidae). Auk 116:141-157.

BROWN, R. E., AND M. R. FEDDE. 1993. Air-flow sensors in the avian wing. Journal of Experimental Biology 179:13-30.

BROWN, T. J., AND P. HANDFORD. 2000. Sound design for vocalizations: quality in the woods, consistency in the fields. Condor 102:81-92.

BURLEY, N. 1981. The evolution of sexual indistinguishability. Pages 121- 137 in Natural Selection and Social Behavior: Recent Research and New Theory (R. D. Alexander and D. W. Tinkle, Eds.). Chiron Press, New York, NY, USA.

BURNS, K. 1998. Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. Auk 115:621-634.

BURTT, E. H., JR., AND A. J. GATZ, JR. 1982. Color convergence: is it only mimetic? American Naturalist 119:738-740.

BUSH, K. L., AND C. STROBECK. 2003. Phylogenetic relationships of the Phasianidae reveals possible non-pheasant taxa. Journal of Heredity 94:472-489.

BUSKIRK, J. V. 1997. Independent evolution of song structure and note structure in American wood warblers. Proceedings of the Royal Society of London B 264:755-761.

BUTLER, R. G. AND D. E. BUCKLEY. 2002. Black Guillemot (*Cepphus grylle*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

BYRD, G. V. AND D R. H. DAY. 1986. The avifauna of Buldir Island, Aleutian Islands. Arctic 39:109-118.

BYRD, G. V., AND J. C. WILLIAMS. 1993. Whiskered Auklet (*Aethia pygmaea*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

CALDAROLA, J., A. DILMAGHANI, J. GAGNON, K. HAYCOCK, J. ROTH, C. SOPER AND E. WASSERMAN. 1998. Statview 5.01 - the ultimate integrated data management and presentation system. SAS Institute Inc., Cary, NC, USA.

CANNELL, P. F. 1988. Techniques for study of avian syringes. Auk 100:289-293.

CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the Genus *Acrocephalus*. Behaviour 74:149-166.

CATCHPOLE, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. Pages 297-319 in Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York, NY, USA.

CHENOWETH, S. F., H. D. RUNDLE, AND M. W. BLOWS. 2008. Genetic constraints and the evolution of display trait sexual dimorphism by natural and sexual selection. American Naturalist 171:22-34.

CHILDRESS, R. B. AND L. A. BENNUN. 2002. Sexual character intensity and its relationship to breeding timing, fecundity and mate choice in the great cormorant *Phalacrocorax carbo lucidus*. Journal of Avian Biology 33:23-30.

CLARK, G. A. 2004. Form and function: the external bird. Pages 3.2-3.18 in Handbook of bird biology (S. Podulka, R. Rohrbaugh and R. Bonney, Eds.). Cornell Lab of Ornithology, Ithaca, NY, USA.

CLARK, G. A., AND J. B. CRUZ. 1989. Functional interpretation of protruding filoplumes in oscines. Condor 91:962-965.

CLEMENTS, J. F. 2007. The Clements checklist of birds of the world. Cornell University Press, Ithaca, NY, USA.

CONOVER, M. R., AND D. E. MILLER. 1980. Rictal bristle function in willow flycatcher. Condor 82:469-471.

COYNE, J. A., AND H. A. ORR. 2004. Speciation. Sinauer, Sunderland, MA, USA.

CRAMP, S. (EDITOR). 1989. Handbook of the birds of Europe the Middle East and North Africa. The birds of the western Palearctic. Vol. 4. Terns to woodpeckers. Reprinted with corrections. Oxford University Press, Oxford, UK.

CROWE, T. M., R. C. K. BOWIE, P. BLOOMER, T. G. MANDIWANA, T. A. J. HEDDERSON, E. RANDI, S. L. PEREIRA, AND J. WAKELING. 2006. Phylogenetics, biogeography and classification of, and character evolution in, gamebirds (Aves : Galliformes):

effects of character exclusion, data partitioning and missing data. Cladistics 22:495-532.

CUERVO, A. M., C. D. CADENA, AND N. KRABBE. 2005. *Scytalopus stilesi,* a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. Auk 122:445-463.

DABELSTEEN, T., O. N. LARSEN, AND S. B. PEDERSEN. 1993. Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. Journal of the Acoustical Society of America 93:2206-2220.

DALE, J. 2000. Ornamental plumage does not signal male quality in red-billed queleas. Proceedings of the Royal Society B 267:2143-2149.

DARWIN, C. 1859. On the origin of species by means of natural selection. Murray, London, UK.

DARWIN, C. 1871. The descent of man and selection in relation to sex. Murray, London, UK.

DAVIS, L. I. 1962. Acoustic evidence of relationships in *Caprimulgus*. Texas Journal of Science 14:72-106.

DAVIS, L. I. 1965. Acoustic evidence of relationship in *Ortalis* (Cracidae). Southwestern Naturalist 10:288-301.

DECHESNE, S. B. C. 1998. Vocalizations of the Marbled Murrelet (*Brachyramphus marmoratus*): vocal repertoire and individuality. M.Sc. dissertation. University of Victoria, BC, Canada.

DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL (EDITORS). 1992-2002. Handbook of the birds of the world. Vols. 1-7. Lynx Edicions, Barcelona, Spain.

DOUGLAS, H. D., J. E. CO, T. H. JONES, AND W. E. CORNER. 2004. Interspecific differences in *Aethia* spp. auklet odorents and evidence for chemical defense against ectoparasites. Journal of Chemical Ecology 30:1921-1931.

DROST, C. A., AND D. B. LEWIS. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

DUMBACHER, J. P., T. K. PRATT, AND R. C. FLEISCHER. 2003. Phylogeny of the Owlet-nightjars (Aves: Aegothelidae) based on mitochondrial DNA sequence. Molecular Phylogenetics and Evolution 29:540-549.

DYKE, G. J., B. E. GULAS, AND T. M. CROWE. 2003. Suprageneric relationships of galliform birds (Aves, Galliformes): A cladistic analysis of morphological characters. Zoological Journal of the Linnean Society 137:227-244.

EMLEN, D. J. 2001. Costs and the diversification of exaggerated animal structures. Science 291:1534-1536.

ENDLER, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, NJ, USA.

ENDLER, J. A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139:S125-S153.

ENDLER, J. A. 1993a. The color of light in forests and its implications. Ecological Monographs 63:1-27.

ENDLER, J. A. 1993b. Some general comments on the evolution and design of animal communication systems. Philosophical Transactions of the Royal Society of London B 340:215-225.

ENDLER, J. A., D. A. WESTCOTT, J. R. MADDEN, AND T. ROBSON. 2005. Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. Evolution 59:1795-1818.

FAIN, M. AND P. HOUDE. 2007. Multilocus perspectives on the monophyly and phylogeny of the order Charadriiformes (Aves). BMC Evolutionary Biology 7:35.

FARABAUGH, S. M. AND R. J. DOOLING. 1996. Acoustic communication in parrots: laboratory and field studies of budgerigars, *Melopsittacus undulatus*. Pages 97-118 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, NY, USA.

FARRIS, J. S., M. KALLERSJO, A. G. KLUGE, AND C. BULT. 1994. Testing significance of incongruence. Cladistics 10:315-319.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1-15.

FENTON, M. B. 1990. The foraging behavior and ecology of animal-eating bats. Canadian Journal of Zoology 68:411-422.

FERDINAND, L. 1969. Some observations on the behaviour of the Little Auk (*Plotus* [sic] *alle)* on the breeding-ground, with special reference to voice production. Dansk Ornitologisk Forenings Tidsskrift 63:19-45.

FISHER, R. A. 1958. The genetical theory of natural selection. Dover, New York, NY, USA.

FLEISHMAN, J. L. 2000. Signal function, signal efficiency and the evolution of anoline lizard dewlap color. Pages 209-236 in Animal signals: signaling an signal design in animal communication (Y. Espmark, T. Amundsen and G. Rosenquist, Eds.). Tapir Academic Press, Trondheim, Norway.

FLETCHER, N. H., AND A. TARNOPOLSKY. 1999. Acoustics of the avian vocal tract. The Journal of the Acoustical Society of America 105:35-49.

FRASER, G. S., I. L. JONES, AND F. M. HUNTER. 2002. Male-female differences in parental care in monogamous Crested Auklets. Condor 104:413-423.

FRIESEN, V. L., A. J. BAKER, AND J. F. PIATT. 1996. Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. Molecular Biology and Evolution 13:359-367.

FRUMHOFF, P. C., AND H. K. REEVE. 1994. Using phylogenies to test hypotheses of adaptation: a critique of some current proposals. Evolution 48:172-180.

FRYXELL, J. M. 1997. Evolutionary dynamics of habitat use. Evolutionary Ecology 11:687-701.

GALEOTTI, P., AND D. RUBOLINI. 2007. Head ornaments in owls: what are their functions? Journal of Avian Biology 38:731-736.

GARAMSZEGI, L. Z., A. P. MØLLER, AND J. ERRITZOE. 2001. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proceedings of the Royal Society of London B 269:961-967.

GASTON, A. J. AND S. B. C. DECHESNE. 1996. Rhinoceros Auklet (*Cerorhinca monocerata*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

GASTON, A. J., AND I. L. JONES. 1998. The auks. Oxford University Press, Oxford, UK.

GIBBS, H. L., AND P. R. GRANT. 1987. Oscillating selection on Darwin's finches. Nature 327:511-513.

GIBSON, J. J. 1998. Visually controlled locomotion and visual orientation in animals. Ecological Psychology 10:161 – 176.

GILLIARD, E. T. 1956. Bower ornamentation versus plumage characters in bowerbirds. Auk 73:450-451.

GITTLEMAN, J. L., AND H. LUH. 1992. On comparing comparative methods. Annual Review of Ecology and Systematics 23:383-404.

GONZAGA, L. P., A. M. P. CARVALHAES, AND D. R. C. BUZZETTI. 2007. A new species of *Formicivora* antwren from the Chapada Diamantina, eastern Brazil (Aves: Passeriformes: Thamnophilidae). Zootaxa 1473:25-44.

GOTTSCHALDT, K. M. 1985. Structure and function of avian somatosensory receptors. Pages 375-462 in Form and function in birds (A. S. King and J. McLelland Eds.), Vol. 3. Academic Press. London, UK.

GRETHER, G. F., AND R. M. GREY. 1996. Novel cost of a sexually selected trait in the rubyspot damselfly *Hetaerina americana*: conspicuousness to prey. Behavioral Ecology 7:465-473.

HAGELIN, J. C., AND J. D. LIGON. 2001. Female quail prefer testosterone-mediated traits, rather than the ornate plumage of males. Animal Behaviour 61:465-476.

HAGELIN, J.C., JONES, I.L, AND L.E.L. RASMUSSEN. 2003. A tangerine scented social odour in a monogamous seabird. Proceedings of the Royal Society B 270:1323-1329.

HAILMAN, J. P. 1977. Optical signals: animal communication and light. Indiana University Press, London, UK.

HAILMAN, J. P. AND M. S. FICKEN. 1996. Comparative analysis of repertoires, with reference to chickadees. Pages 136-159 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, NY, USA.

HAILMAN J. P., M. S. FICKEN, AND R. W. FICKEN. 1985. The 'chick-a-dee' calls of *Parus atricapillus*: a recombinant system of animal communication compared with English. Semiotica 56:191-224.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384-387.

HANSELL, M. H. 2000. Bird nests and construction behaviour. Cambridge University Press, Cambridge, UK.

HART, N. S. 2001. The visual ecology of avian photoreceptors. Progress in Retinal and Eye Research 20:675-703.

HARVEY, P. H., AND J. R. KREBS. 1990. Comparing brains. Science 249:140-146.

HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, London, UK.

HODOS, W. 1993. The visual capabilities of birds. Pages 63-76 in Vision, brain, and behavior in birds (H. P. Zeigler and H. Bischof, Eds.). MIT Press, Cambridge, MA, USA.

HÖGLUND, J. 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. American Naturalist 134:72-87.

HÖGLUND, J., AND B. SILLÉN-TULLBERG. 1994. Does lekking promote the evolution of male-biased size dimorphism in birds? On the use of comparative approaches. American Naturalist 144:881-889.

HUGHES, J. M., AND A. J. BAKER. 1999. Phylogenetic relationships of the enigmatic hoatzin (*Opisthocomus hoatzin*) resolved using mitochondrial and nuclear gene sequences. Molecular Biology and Evolution 16:1300-1307.

HUNTER, F. M., AND I. L. JONES. 1999. The frequency and function of aquatic courtship and copulation in Least, Crested, Whiskered, and Parakeet Auklets. Condor 101:518-528.

HUNTER, F. M., I. L. JONES, J. C. WILLIAMS, AND G. V. BYRD. 2002. Breeding biology of the Whiskered Auklet (*Aethia pygmaea*) at Buldir Island, Alaska. Auk 119:1036-1051.

HUNTER, M. L., AND J. R. KREBS. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. Journal of Animal Ecology 48:759-785.

HUXLEY, J. S. 1931. Biology of bird courtship. Proceedings of the International Ornithological Congress 7:107-108.

HUXLEY, J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. American Naturalist 72:416-433.

HUXLEY, J. 1966. A discussion on ritualization of behavior in animals and man. Philosophical Transactions of the Royal Society of London B 251:249-271.

IRWIN, R. E. 1996. The phylogenetic content of avian courtship display and song evolution. Pages 234-252 in Phylogenies and the comparative method in animal behavior (E. P. Martins, Ed.). Oxford University Press, Oxford, UK.

IRWIN, D. E. 2000. Song variation in an avian ring species. Evolution 54:998-1010.

ISLER, M. L., P. R. ISLER, AND R. T. BRUMFIELD. 2005. Clinal variation in vocalizations of an antbird (Thamnophilidae) and implications for defining species limits. Auk 122:433-444.

ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 2007. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. Auk 124:11-28.

IWASA, Y., AND A. POMIANKOWSKI. 1994. The evolution of mate preferences for multiple sexual ornaments. Evolution 48:853-867.

JACKSON, H. D. 2003. A review of foraging and feeding behaviour, and associated anatomical adaptations, in Afrotropical nightjars. Ostrich 74:187-204.

JACOBS, L. F., S. J. C. GAULIN, D. F. SHERRY, AND G. E. HOFFMAN. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. Proceedings of the National Academy of Sciences USA 87:6349-6352.

JAMES, P. C. 1986. The filoplumes of the Manx Shearwater *Puffinus puffinus*. Bird Study 33:117-120.

JARVIS, E. D. 2006. Evolution of brain structures for vocal learning in birds: a synopsis. Acta Zoologica Sinica 52:85-89.

JOHNSTONE, R. A. 1996. Multiple displays in animal communication: 'backup signals' and 'multiple messages'. Philosophical Transactions of the Royal Society of London B 351:329-338.

JOHNSON, K. P. 1999. The evolution of bill coloration and plumage dimorphism supports the transference hypothesis in dabbling ducks. Behavioral Ecology 10:63-67.

JOHNSON, K. P., AND D. H. CLAYTON. 2000. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). Molecular Phylogenetics and Evolution 14:141-151.

JOHNSON, K. P., F. MCKINNEY, R. WILSON, AND M. D. SORENSON. 2000. The evolution of postcopulatory displays in dabbling ducks (Anatini): a phylogenetic perspective. Animal Behaviour 59:953-963.

JONES, I. L. 1990. Plumage variability functions for status signalling in Least Auklets. Animal Behaviour 39:967-975.

JONES, I. L. 1993a. Crested Auklet (*Aethia cristatella*). in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences: American Ornithologists' Union, Washington, DC, USA.

JONES, I. L. 1993b. Least Auklet (*Aethia pusilla*). in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences: American Ornithologists' Union, Washington DC, USA.

JONES, I. L. 1993c. Sexual differences in bill shape and external measurements of the Crested Auklet. Wilson Bulletin 105:525-529.

JONES, I. L. 1999. Assessing the role of sexual selection in adaptive radiation of the auklets (Alcidae, Aethiini). Proceedings of the International Ornithological Congress 22:1115-1125.

JONES, I. L., AND R. MONTGOMERIE. 1991. Mating and remating of Least Auklets *Aethia pusilla* relative to ornamental traits. Behavioral Ecology 2:249-257.

JONES, I. L., AND R. MONTGOMERIE. 1992. Least Auklet ornaments: do they function as quality indicators? Behavioral Ecology and Sociobiology 30:43-52.

JONES, I. L., AND F. M. HUNTER. 1993. Mutual sexual selection in a monogamous seabird. Nature 362:238-239.

JONES, I. L., AND F. M. HUNTER. 1998. Heterospecific mating preferences for a feather ornament in Least Auklets. Behavioral Ecology 9:189-192.

JONES, I. L., AND F. M. HUNTER. 1999. Experimental evidence for mutual inter- and intra-sexual selection favouring a Crested Auklet ornament. Animal Behaviour 57:521-528.

JONES, I. L., J. B. FALLS, AND A. J. GASTON. 1987. Vocal recognition between parents and young of Ancient Murrelets (*Synthliboramphus antiquus*). Animal Behaviour 35:1405-1415.

JONES, I. L., J. B. FALLS, AND A. J. GASTON. 1989a. The vocal repertoire of the Ancient Murrelet (*Synthliboramphus antiquus*). Condor 91:699-710.

JONES, I. L., A. J. GASTON, AND J. B. FALLS. 1989b. Factors affecting colony attendance by Ancient Murrelets (*Synthliboramphus antiquus*). Canadian Journal of Zoology 68:433-441.

JONES, I. L., F. M. HUNTER, AND G. FRASER. 2000. Patterns of variation in ornaments of Crested Auklets *Aethia cristatella*. Journal of Avian Biology 31:119-127.

JONES, I. L., S. ROWE, AND F. MEHLUM. 2002. Social and self-maintenance behaviour of adult and sub-adult Little Auks *Alle alle* and Least Auklets *Aethia pusilla* at two breeding colonies. Ibis 144:113-117.

JONES, I. L., N. B. KONYUKHOV, J. C. WILLIAMS, AND G. V. BYRD. 2001. Parakeet Auklet (*Aethia psittacula*). In The Birds of North America (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia, PA, USA.

JONES, I. L., J. C. HAGELIN, H. L. MAJOR, AND L. E. L. RASMUSSEN. 2004a. An experimental field study of the function of Crested Auklet feather odor. Condor 106:71-78.

JONES, I. L., F. M. HUNTER, G. J. ROBERTSON, AND G. FRASER. 2004b. Natural variation in the sexually selected feather ornaments of Crested Auklets (*Aethia cristatella*) does not predict future survival. Behavioral Ecology 15:332-337.

JONES, I. L., F. M. HUNTER, G. J. ROBERTSON, J. C. WILLIAMS, AND G. V. BYRD. 2007. Covariation among demographic and climate parameters in Whiskered Auklets *Aethia pygmaea*. Journal of Avian Biology 38:450-461.

JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. Springer, Berlin, Germany.

KANESHIRO, K. Y. 1988. Speciation in the Hawaiian *Drosophila*: sexual selection appears to play an important role. BioScience 38:258-263.

KENNEDY, M., R. D. GRAY, AND H. G. SPENCER. 2000. The phylogenetic relationships of the shags and cormorants: can sequence data resolve a disagreement between behavior and morphology? Molecular Phylogenetics and Evolution 17:345-359.

KHARITONOV, S. P. 1980. Materials on birds of Iona Island. Ornitologiya 15:10-15.

KING, A. S. 1989. Functional anatomy of the avian syrinx. Pages 105-192 in Form and function in birds (A. S. King and J. McLelland, Eds.). Academic Press, London, UK.

KIRCHMAN, J. J., S. J. HACKETT, S. M. GOODMAN, AND J. M. BATES. 2001. Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. Auk 118:849-863.

KIRKPATRICK, M. 1982. Sexual selection and the evolution of mate choice. Evolution 36:1-12.

KIRKPATRICK, M. 1987. Sexual selection by female choice in polygynous animals. Annual Review of Ecology and Systematics 18:43-70.

KIRKPATRICK, M., AND M. J. RYAN. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350:33-38.

KIRKPATRICK, M., T. PRICE, AND S. J. ARNOLD. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. Evolution 44:180-193.

KLEVEN, O., F. JACOBSEN, R. IZADNEGAHDAR, R. J. ROBERTSON, AND J. T. LIFJELD. 2006. Male tail streamer length predicts fertilization success in the North American Barn Swallow (*Hirundo rustica erythrogaster*). Behavioral Ecology and Sociobiology 59:412-418.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phylogenetics and the evolution of anurans. Systematic Zoology 18:1-32.

KONYUKHOV, N. B. 2001. Molting and seasonal bill-plate shedding in the Whiskered Auklet (*Aethia pygmaea*). Biology Bulletin 28:266-277.

KORT, S. R. D., AND C. TEN CATE. 2004. Repeated decrease in vocal repertoire size in *Streptopelia* doves. Animal Behaviour 67:549-557.

KOTIAHO, J. S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biological Reviews 76:365-376.

KREBS, J. R., AND N. B. DAVIES. 1991. Behavioral ecology: an evolutionary approach (3rd ed). Blackwell, London, UK.

KREBS, J. R., D. F. SHERRY, S. D. HEALY, V. H. PERRY, AND A. L. VACCARINO. 1989. Hippocampal specialization of food-storing birds. Proceedings of the National Academy of Sciences USA 86:1388-1392.

KRESS, S. W. 1997. Using animal behavior for conservation: case studies in seabird restoration from the Maine coast, USA. Journal of the Yamashina Institute for Ornithology 29:1-26.

KROODSMA, D. E., AND R. A. CANDY. 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among Marsh Wren populations have a genetic basis. Auk 102:439-446.

KUSMIERSKI, R., G. BORGIA, R. H. CROZIER, AND B. H. Y. CHAN. 1993. Molecular information on bowerbird phylogeny and the evolution of exaggerated male characteristics. Journal of Evolutionary Biology 6:737-752.

KÜSTER, E. 1905. Die innervation und entwicklung der tastfeder. Morphol Jahrb 34:126-148.

LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292-305.

LANDE, R. 1981. Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences USA 78:3721-3725.

LANDE, R., AND S. J. ARNOLD. 1985. Evolution of mating preference and sexual dimorphism. Journal of Theoretical Biology 117:651-664.

LANYON, W. E. 1969. Vocal characters and avian systematics. Pages 291-310 in Bird vocalizations (R. A. Hinde, Ed.). Cambridge University Press, Cambridge, UK.

LANYON, S. M. 1992. Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. Science 255:77-79.

LARSEN, C., M. SPEED, N. HARVEY, AND H. A. NOYES. 2007. A molecular phylogeny of the nightjars (Aves: Caprimulgidae) suggests extensive conservation of primitive morphological traits across multiple lineages. Molecular Phylogenetics and Evolution 42:789-796.

LEDERER, R. J. 1972. Role of avian rictal bristles. Wilson Bulletin 84:193-197.

LEFEVRE, D. S. AND D. SIEGEL-CAUSEY. 1993. First report on bird remains from Buldir Island, Aleutian Islands, Alaska. Archaeofauna 2:83-96.

LEFEVRE, K., A. J. GASTON, AND R. MONTGOMERIE. 2001. Repertoire, structure, and individual distinctiveness of Thick-billed Murre calls. Condor 103:134-142.

LIEBMAN, P. A. 1972. Microspectrophotometry of photoreceptors. Pages 481-528 in Handbook of sensory physiology, photochemistry of vision (H. L. A. Dartnall, Ed.). Springer. Berlin, Germany.

LIGON, J. D. AND P. W. ZWARTJES. 1995. Ornate plumage of male red junglefowl does not influence mate choice by females. Animal Behaviour 49:117-125.

LIVEZEY, B. 1997. A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. Annals of Carnegie Museum 66:457-496.

LIVEZEY, B. C., AND R. L. ZUSI. 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. Zoological Journal of the Linnean Society 149:1-95.

LOREK, G. 1992. Why owls have ear tufts? Przeglad Zoologiczny 36:181-186.

LORENZ, K. 1970. Contributions to the study of the ethology of social Corvidae (1931). Pages 1-56 in Studies in animal and human behaviour (R. Martin, Ed.). Harvard University Press, Cambridge, MA, USA.

LORENZ, K. 1971. Comparative studies of the motor patterns of Anatinae (1941). Pages 14-106 in Studies in Animal and Human Behaviour (R. Martin, Eds.). Harvard University Press, Cambridge, MA, USA.

LOWTHER, P. E., A. W. DIAMOND, S. W. KRESS, G. J. ROBERTSON, AND K. RUSSELL. 2002. Atlantic Puffin (*Fratercula arctica*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

LUCAS A. M., AND P. R. STETTENHEIM. 1972. Structure of feathers. Pages 341-419 in Avian anatomy–integument. US Department of Agriculture Handbook 362, Washington, DC, USA.

MCGUIRE, J. A., C. C. WITT, D. L. ALTSHULER, AND J. V. REMSEN, JR. 2007. Phylogenetic systematics and biogeography of hummingbirds: bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. Systematic Biology 56:837-856.

MADDISON, W. P. 1990. A method for testing the correlated evolution of two binary characters are gains or losses concentrated on certain branches of a phylogenetic tree. Evolution 44:539-557.

MADDISON, W. P., AND D. R. MADDISON. 1992. MACCLADE 3.04: analysis of phylogeny and character evolution. Sinauer, Sunderland, MA, USA.

MANDELIK, Y., M. JONES, AND T. DAYAN. 2003. Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. Evolutionary Ecology Research 5:501-515.

MANUWAL, D. A., AND A. C. THORESEN. 1993. Cassin's Auklet (*Ptychoramphus aleuticus*). in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences: American Ornithologists' Union, Washington DC, USA.

MARIAUX, J., AND M. J. BRAUN. 1996. A molecular phylogenetic survey of the nightjars and allies (Caprimulgiformes) with special emphasis on the potoos (Nyctibiidae). Molecular Phylogenetics and Evolution 6:228-244.

MARKS, B. D., AND D. E. WILLARD. 2005. Phylogenetic relationships of the Madagascar Pygmy Kingfisher (*Ispidina madagascariensis*). Auk 122:1271-1280.

MARLER, P. 1955. Characteristics of some animal calls. Nature 176:6-7.

MARLER , P. AND R. PICKERT. 1984. Species-universal microstructure in the learned song of the Swamp Sparrow (*Melospiza georgiana*). Animal Behaviour 32:673-689.

MARLER, P. AND H. SLABBEKOORN (EDITORS). 2004. Nature's music: the science of birdsong. Academic Press, New York, NY, USA.

MARTEN, K., D. QUINE, AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. Behavioral Ecology and Sociobiology 2:291-302.

MARTENS, J. 1996. Vocalizations and speciation of Palearctic birds. Pages 221-240 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York, USA.

MARTIN, G. R. 1990. Birds by night. T & AD Poyser, London, UK.

MARTIN, G., L. ROJAS, Y. RAMÍREZ, AND R. MCNEIL. 2004. The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity. Naturwissenschaften 91:26-29.

MARTINS, E. P. 2000. Adaptation and the comparative method. Trends in Ecology and Evolution 15:296-299.

MARTINS, E. P. (EDITOR). 1996. Phylogenies and the comparative method in animal behavior. Oxford University Press, New York, NY, USA.

MARTINS, E. P., AND T. F. HANSEN. 1996. Statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. Pages 22-75 in Phylogenies and the comparative method in animal behavior (E. P. Martins, Ed.). Oxford University Press, Oxford, UK.

MASTERS, J. C. 2007. Taking phylogenetics beyond pattern analysis: can models of genome dynamics guide predictions about homoplasy in morphological and behavioral data sets? Journal of Human Evolution 52:522-535.

MAYNARD-SMITH, J. 1985. Sexual selection, handicaps and true fitness. Journal of Theoretical Biology 115:1-8.

MAYR, E. 1940. Speciation phenomena in birds. American Naturalist 74:249.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA, USA.

MCCRACKEN, K. G. AND F. H. SHELDON. 1997. Avian vocalizations and phylogenetic signal. Proceedings of the National Academy of Sciences USA 94:3833-3836.

MILLER, E. H. 1996. Acoustic differentiation and speciation in shorebirds. Pages 241-257 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, NY, USA.

MILLER, E. H., S. S. SENEVIRATNE, I. L. JONES, G. J. ROBERTSON, AND S. I. WILHELM. 2008. Syringeal anatomy and allometry in murres (Alcidae: *Uria*). Journal of Ornithology. DOI 10.1007/s10336-008-0304-z (advanced online edition).

MISKELLY, C. M. AND G. A. TAYLOR. 2004. Establishment of a colony of Common Diving Petrels (*Pelecanoides urinatrix*) by chick transfers and acoustic attraction. Emu 104:205-211.

MØLLER, A. P. 1991. Sexual selection in the monogamous Barn Swallow (*Hirundo rustica*). I. Determinants of tail ornament size. Evolution 45:1823-1836.

MØLLER, A. P. 1993. Sexual selection in the Barn Swallow *Hirundo rustica*: III. Female tail ornaments. Evolution 47:417-431.

MØLLER, A. P., F. DE LOPE, AND J. M. LOPEZ CABALLERO. 1995. Foraging costs of a tail ornament: Experimental evidence from two populations of Barn Swallows *Hirundo rustica* with different degrees of sexual size dimorphism. Behavioral Ecology and Sociobiology 37:289-295.

MØLLER, A. P., AND T. R. BIRKHEAD. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. American Naturalist 139:644-656.

MØLLER, A. P., AND J. J. CUERVO. 1998. Speciation and feather ornamentation in birds. Evolution 52:859-869.

MOUM, T., U. ARNASON, AND E. ARNASON. 2002. Mitochondrial DNA sequence evolution and phylogeny of the Atlantic Alcidae, including the extinct Great Auk (*Pinguinus impennis*). Molecular Biology and Evolution 19:1434-1439.

MOUM, T., S. JOHANSEN, K. E. ERIKSTAD, AND J. F. PIATT. 1994. Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. Proceedings of the National Acadamy of Sciences USA 91:7912-7916.

MOYLE, R. G. 2004. Phylogenetics of barbets (Aves: Piciformes) based on nuclear and mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 30:187-200.

MOYLE, R. G. 2005. Phylogeny and biogeographical history of Trogoniformes, a pantropical bird order. Biological Journal of the Linnean Society 84:725-738.

NELSON, D. A. 1985. The syntactic and semantic organization of Pigeon Guillemot (*Cepphus columba*) vocal behavior. Zeitschrift für Tierpsychologie 67:97-130.

NELSON, S. K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1996. Applied linear statistical models: regression, analysis of variance, and experimental designs. 4th ed. Irwin, Chicago, IL USA.

NEUWEILER, G. 1989. Foraging ecology and audition in echolocating bats. Trends in Ecology and Evolution 4:160-166.

NICHOLLS, J. A,.AND A. W. GOLDIZEN. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. Journal of Animal Ecology 75:549-558.

NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia Chiroptera): wing adaptations, flight performance foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316:335-427.

NOTTEBOHM, F. 1972. The origins of vocal learning. American Naturalist 106:116-140.

OAKES, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: comparative approaches. American Naturalist 140:665-684.

OMLAND, K. E. 1994. Character congruence between a molecular and a morphological phylogeny for dabbling ducks (*Anas*). Systematic Biology 43:369-386.

OMLAND, K. E., AND S. M. LANYON. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. Evolution 54:2119-2133.

OVERTON, L. C., AND D. D. RHOADS. 2004. Molecular phylogenetic relationships based on mitochondrial and nuclear gene sequences for the todies (*Todus*, Todidae) of the Caribbean. Molecular Phylogenetics and Evolution 32:524-538.

PÄCKERT, M., J. MARTENS, J. KOSUCH, A. A. NAZARENKO, AND M. VEITH. 2003. Phylogenetic signal in the song of crests and kinglets (Aves: *Regulus*). Evolution 57:616-629.

PAGEL, M. D., AND P. H. HARVEY. 1988. Recent developments in the analysis of comparative data. Quarterly Review of Biology 63:413-440.

PARK, O., A. BARDEN, AND E. WILLIAMS. 1940. Studies in nocturnal ecology IX. Further analysis of activity of Panama rain forest animals. Ecology 21:122-134.

PARKER, T. H., J. C. HAGELIN, AND J. D. LIGON. 2005. Do female *Callipepla* quail respond to male plumage ornaments? Animal Behaviour 70:e7-e9.

PATON, T. A., AND A. J. BAKER. 2006. Sequences from 14 mitochondrial genes provide a well-supported phylogeny of the Charadriiform birds congruent with the nuclear RAG-1 tree. Molecular Phylogenetics and Evolution 39:657-667.

PATON, T., A. J. BAKER, J. G. GROTH, AND G. F. BARROWCLOUGH. 2003. RAG-1 sequences resolve phylogenetic relationships within Charadriiform birds. Molecular Phylogenetics and Evolution 29:268-278.

PAYNE, R. B. 1986. Bird songs and avian systematics. Current Ornithology 3:87-126.

PEREIRA, S. L., AND A. J. BAKER. 2004. Vicariant speciation of curassows (Aves, Cracidae): a hypothesis based on mitochondrial DNA phylogeny. Auk 121:682-694.

PEREIRA, S. L., AND A. J. BAKER. 2008. DNA evidence for a Paleocene origin of the Alcidae (Aves: Charadriiformes) in the Pacific and multiple dispersals across northern oceans. Molecular Phylogenetics and Evolution 46:430-445.

PERRONE, M., JR. 1981. Adaptive significance of ear tufts in owls. Condor 83:383-384.

PERRY, E. A., S. M. CARR, S. E. BARTLETT, AND W. S. DAVIDSON. 1995. A phylogenetic perspective on the evolution of reproductive behavior in pagophilic seals of the northwest Atlantic as indicated by mitochondrial sequences. Journal of Mammalogy 76:22-31.

PIATT, J. F. AND A. S. KITAYSKY. 2002a. Horned Puffin (*Fratercula corniculata*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

PIATT, J. F. AND A. S. KITAYSKY. 2002b. Tufted Puffin (*Fratercula cirrhata*). in The Birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences: The American Ornithologists' Union, Washington, DC, USA.

PITOCCHELLI, J., J. F. PIATT, AND H. R. CARTER. 2003. Variation in plumage, molt, and morphology of the Whiskered Auklet (*Aethia pygmaea*) in Alaska. Journal of Field Ornithology 74:90-98.

PLENGE, M., E. CURIO, AND K. WITTE. 2000. Sexual imprinting supports the evolution of novel male traits by transference of a preference for the colour red. Behaviour 137:741-758.

PODOS, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. Nature 409:185-188.

POMIANKOWSKI, A. 1988. The evolution of female mate preferences for male genetic quality. Oxford Surveys in Evolutionary Biology 5:136-184.

POST, E., R. LANGVATN, M. C. FORCHHAMMER, AND N. C. STENSETH. 1999. Environmental variation shapes sexual dimorphism in red deer. Proceedings of the National Academy of Sciences USA 96:4467-4471.

PREZIOSI, R. F., AND D. J. FAIRBAIRN. 1996. Sexual size dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: body size, components of body size and male mating success. Journal of Evolutionary Biology 9:317-336.

PRICE, T. 1997. Correlated evolution and independent contrasts. Philosophical Transactions of the Royal Society of London B 352:519-529.

PRICE, T. 1998. Sexual selection and natural selection in bird speciation. Philosophical Transactions of the Royal Society of London B 353:251-260.

PRICE, J. J., AND S. M. LANYON. 2002. Reconstructing the evolution of complex bird song in the oropendolas. Evolution 56 1514-1529.

PRYKE, S. R., AND S. ANDERSSON. 2005. Experimental evidence for female choice and energetic costs of male tail elongation in red-collared widowbirds. Biological Journal of the Linnean Society 86:35-43.

PURVIS, A., AND A. RAMBAUT. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. Computer Applications in the Biosciences 11:247-251.

QVARNSTROEM, A., J. E. BROMMER, AND L. GUSTAFSSON. 2006. Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. Nature 441:84-86.

RIDLEY, M., AND A. GRAFEN. 1996. How to study discrete comparative methods. Pages 76-103 in Phylogenies and the comparative method in animal behaviour (E. P. Martins, Ed.). Oxford University Press, Oxford, UK.

RILOV, G., W. F. FIGUEIRA, S. J. LYMAN, AND L. B. CROWDER. 2007. Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. Marine Ecology Progress Series 329:225-238.

ROBERTS, J., A. MORENO, A. KACELNIK, AND M. HUNTER. 1983. Physical considerations in the frequency limits of birdsong. Acoustics Letters 6:100-105.

ROWE, L. V., M. R. EVANS, AND K. L. BUCHANAN. 2001. The function and evolution of the tail streamer in Hirudinea. Behavioral Ecology 12:157-163.

RYAN, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. Oxford Surveys in Evolutionary Biology 7:157-195.

RYAN, M. J. 1996. Phylogenetics in behavior: some cautions and expectations. Pages 1-21 in Phylogenetics and the comparative method in animal behavior (E. P. Martins, Ed.). Oxford University Press, New York, NY, USA.

RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126:87-100.

RYAN, M. J., AND A. S. RAND. 1993. Species recognition and sexual selection as a unitary problem in animal communication. Evolution 47:647-657.

RYAN, M. J., J. FOX, W. WILCZYNSKI, AND A. S. RAND. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343:66-67.

RYU, S. H., AND H. C. PARK. 2003. Molecular phylogeny of the family Strigidae (Aves) based on mitochondrial cytochrome b gene. Korean Journal of Systematic Zoology 19:297-304.

SAFI, K., AND D. K. N. DECHMANN. 2005. Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). Proceedings of the Royal Society B 272:179-186.

SCHILDMACHER, H. 1931. Untersuchungen über die funktion der herbstschen körperchen. Journal of Ornithology 79:374-415.

SCHLUTER, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist 156:S4-S16.

SCHLUTER, D., AND J. N. M. SMITH. 1986. Natural selection on beak and body size in the Song Sparrow *Melospiza melodia*. Evolution 40:221-231.

SCHLUTER, D., AND P. J. WEATHERHEAD. 1990. Targets of sexual selection: song and plumage of wood warblers. Evolution 44:1967-1977.

SCHLUTER, D., T. D. PRICE, AND L. ROWE. 1991. Conflicting selection pressures and life-history trade-offs. Proceedings of the Royal Society of London B 246:11-17.

SEDDON, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. Evolution 59 200-215.

SENEVIRATNE, S. S., AND I. L. JONES. 2008. Mechanosensory function for facial ornamentation in the Whiskered Auklet, a crevice-dwelling seabird. Behavioral Ecology 19:784-790.

SENEVIRATNE, S. S., I. L. JONES, E. H. MILLER AND S. M. CARR. 2008. Vocal repertoires of auklets (Alcidae: Aethiini): structural organization and categorization. Wilson Journal of Ornithology (in revision).

SEARCY, W. A., AND K. YASUKAWA. 1996. Song and female choice. Pages 454-473 in Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, NY, USA.

SHELLEY, E. L. AND D. T. BLUMSTEIN. 2005. The evolution of vocal alarm communication in rodents. Behavioral Ecology 16:169-177.

SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism - a review of the evidence. Quarterly Review of Biology 64:419-461.

SIBLEY, C. G. 1957. The Evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor 59:166-191.

SKROBLIN, A., AND M. W. BLOWS. 2006. Measuring natural and sexual selection on breeding values of male display traits in *Drosophila serrata*. Journal of Evolutionary Biology 19:35-41.

SLABBEKOORN, H. 2004. Singing in the wild: the ecology of birdsong. Pages 178-205 in Nature's music: the science of birdsong (P. Marler, and H. Slabbekoorn, Eds.). Elsevier Acedamic Press, London, UK.

SLABBEKOORN, H., AND T. B. SMITH. 2002a. Bird song, ecology and speciation. Philosophical Transactions of the Royal Society of London B 357:493-503.

SLABBEKOORN, H., AND T. B. SMITH. 2002b. Habitat-dependent song divergence in the Little Greenbul: An analysis of environmental selection pressures on acoustic signals. Evolution 56:1849-1858.

SLABBEKOORN, H., S. D. KORT, AND C. T. CATE. 1999. Comparative analysis of perch-coo vocalizations in *Streptopelia* doves. Auk 116:737-748.

SPEARMAN, R. I. C., AND J. A. HARDY, 1985. Integument. Pages 1-56 in Form and function in birds (A. S. King, and J. McLelland, Eds.) Vol. 3. Academic Press, London, UK.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, NY, USA.

SORENSON, M. D., AND T. W. QUINN. 1998. Numts: a challenge for avian systematics and population biology. Auk 115:214-221.

STEARNS, S. C. 1989. The evolutionary significance of phenotypic plasticity. BioScience 39:436-445.

STEARNS, S., G. DE JONG, AND B. NEWMAN. 1991. The effects of phenotypic plasticity on genetic correlations. Trends in Ecology and Evolution 6:122-126.

STETTENHEIM P. 1972. The integument of birds. Pages 2-54 in Avian biology (D. S. Farner and J. R. King Eds.) Vol 3. Academic Press, New York, USA.

STRAUCH, J. G. 1985. The phylogeny of the Alcidae. Auk 102 520-539.

STRIJBOS, J. P. 1927. Camouflage van *Caprimulgus europaeus* L. Ardea 16:46.

SUNG, H., E. H. MILLER, AND S. P. FLEMMING. 2005. Breeding vocalizations of the Piping Plover (*Charadrius melodus*): structure, diversity, and repertoire organization. Canadian Journal of Zoology 83:579-595.

SWADDLE, J. P., AND M. S. WITTER. 1998. Cluttered habitats reduce wing asymmetry and increase flight performance in european starlings. Behavioral Ecology and Sociobiology 42:281-287.

SWOFFORD, D. L. 2002. PAUP: phylogenetic analysis using parsimony. Version 4.0b. Sinauer, Sunderland, MA, USA.

TAKAHASHI, M., H. ARITA, M. HIRAIWA-HASEGAWA, AND T. HASEGAWA. 2008. Peahens do not prefer peacocks with more elaborate trains. Animal Behaviour 75:1209-1219.

THOMAS, G. H., M. A. WILLS, AND T. SZÉKELY. 2004a. Phylogeny of shorebirds, gulls, and alcids (Aves: Charadrii) from the cytochrome-b gene: parsimony, Bayesian inference, minimum evolution, and quartet puzzling. Molecular Phylogenetics and Evolution 30:516-526.

THOMAS, G. H., M. A. WILLS, AND T. SZÉKELY. 2004b. A supertree approach to shorebird phylogeny. BMC Evolutionary Biology 4:28.

THOMASSEN, H. A., R. J. DEN TEX, M. A. G. DE BAKKER, AND G. D. E. POVEL. 2005. Phylogenetic relationships amongst swifts and swiftlets: a multi locus approach. Molecular Phylogenetics and Evolution 37:264-277.

THORESEN, A. C. 1964. The breeding behavior of the Cassin's Auklet. Condor 66:456-476.

TINBERGEN, N. 1959. Comparative study of the behaviour of gulls (Laridae): a progress report. Behaviour 15:1-70.

TUBARO, P. L., AND E. T. SEGURA. 1995. Geographic, ecological and subspecific variation in the song of the Rufous-Browed Peppershrike (*Cyclarhis gujanensis*). Condor 97:792-803.

UY, J. A. C., AND G. BORGIA. 2000. Sexual selection drives rapid divergence in bowerbird display traits. Evolution 54:273-278.

VAN TETS, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithological Monographs 2:1-88.

VAN TUINEN, M., C. G. SIBLEY, AND S. B. HEDGES. 1998. Phylogeny and biogeography of ratite birds inferred from DNA sequence of the mitochondrial ribosomal genes. Molecular Biology and Evolution 15:370-376.

VERON, G., AND B. J. WINNEY. 2000. Phylogenetic relationships within the turacos (Musophagidae). Ibis 142:446-456.

WALLACE, A. R. 1878. Tropical nature and other essays. MacMillan, London, UK.

WARNER, R. W. 1969. The anatomy of the avian syrinx. Ph.D. dissertation, University of London, London, UK.

WATADA, M., R. KAKIZAWA, N. KURODA, AND S. UTIDA. 1987. Genetic differentiation and phylogenetic relationships of an avian family, Alcidae (auks). Journal of Yamashima Institute for Ornithology 19:79-88.

WEBB, D. M., AND W. S. MOORE. 2005. A phylogenetic analysis of woodpeckers and their allies using 12S, Cyt b, and COI nucleotide sequences (class Aves; order Piciformes). Molecular Phylogenetics and Evolution 36:233-248.

WENZEL, J. W. 1992. Behavioral homology and phylogeny. Annual Review of Ecology and Systematics 23:361-381.

WEST-EBERHARD, M. J. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58:155-183.

WESTOBY, M., M. R. LEISHMAN, AND J. M. LORD. 1995. On misinterpreting the `phylogenetic correction'. Journal of Ecology 83:531-534.

WHITFIELD, D. P. 1987. Plumage variability, status signaling and individual recognition in avian flocks. Trends in Ecology and Evolution 2:13-18.

WHITFIELD, D. P., AND P. S. TOMKOVICH. 1996. Mating system and timing of breeding in Holarctic waders. Biological Journal of the Linnean Society 57:277-290.

WIENS, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. Trends in Ecology and Evolution 16:517-523.

WILEY, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. American Naturalist 138:973-993.

WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pages 131-181 in Acoustic communication in birds, Vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York, NY, USA.

WILKINSON, G. S. 1987. Equilibrium analysis of sexual selection in *Drosophila melanogaster*. Evolution 41:11-21.

WIMBERGER, P. H., AND A. D. QUEIROZ. 1996. Comparing behavioral and morphological characters as indicators of phylogeny. Pages 206-233 in Phylogenies and the comparative method in animal behavior (E. P. Martins, Ed.). Oxford University Press, Oxford, UK.

WINKLER, H. AND L. SHORT. 1978. A comparative analysis of acoustical signals in Pied Woodpeckers (Aves: *Picoides*). Bulletin of the American Museum of Natural History 160:1-110.

WITTE, K., AND E. CURIO. 1999. Sexes of a monomorphic species differ in preference for mates with a novel trait. Behavioral Ecology 10:15-21.

WRIGHT, D., S. KERJE, H. BRANDSTROM, K. SCHUTZ, A. KINDMARK, L. ANDERSSON, P. JENSEN, AND T. PIZZARI. 2008. The genetic architecture of a female sexual ornament. Evolution 62:86-98.

ZAHAVI, A. 1975. Mate selection: a selection for a handicap. Journal of Theoretical Biology 53:205-214.

ZUBAKIN, V. A., AND N. B. KONYUKHOV. 1999. Biology of reproduction of the Whiskered Auklet (*Aethia pygmaea*): pattern of nesting, activity in the colony, and social behavior. Biology Bulletin 26:460-468.

ZUBAKIN, V. A., AND N. B. KONYUKHOV. 2001. Breeding biology of the Whiskered Auklet (*Aethia pygmaea*): postnesting period. Biology Bulletin 28:31-39.